A BEHAVIORAL AND PERCEPTUAL STUDY OF CAT FLEA LARVAE, *Ctenocephalides felis*, AND THEIR RESPONSES TO VARIOUS STIMULI

By

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This dissertation is dedicated to the Angels we know as ‘Guardians’.

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Abstract of Dissertation Presented to the Graduate School
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A BEHAVIORAL AND PERCEPTUAL STUDY OF CAT FLEA LARVAE, *Ctenocephalides felis,* AND THEIR RESPONSES TO VARIOUS STIMULI

By

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Cat flea larvae, *Ctenocephalides felis*, were found to exhibit an orientation response toward a human stimulus. This is the first report describing this behavior in the cat flea larva. The response was first observed and tested throughout this study in a covered plastic petri dish, and was determined to occur over relatively short distances of up to 2 meters from a human being sitting in a chair. The orientation response could be enhanced by increasing the numbers of cat flea larvae in an experiment.

Cat flea larvae were additionally found to react to magnetic fields of approximately 750 Gauss and electric field intensities of 4.1×10^{-3} V/m, which were discovered to alter the orientation response if tested in conjunction with a human stimulus. The presence of two types of magnets when placed between the fleas and the human stimulus adversely affected the orientation response, which resulted in random movement about the petri dish. The same result was achieved with wind produced from a small fan positioned so as to pass air across the surface of the petri dish. Random behavior, or non-directional movement, was additionally noted when the flea larvae were placed above head level. Cat flea larvae could locate and orient to a human stimulus below head level, but the response was reduced at much lower levels such as ground level.

The cause of this orientation response may be mediated in part or in whole by electromagnetic frequencies of unknown origin. This possibility was theoretically analyzed in reference to external larval morphology. The cat flea's body as well as two of its components, the antenna and the body setae, are certainly capable of receiving complex electromagnetic messages. Detection of electromagnetic radiation may be operating individually or in concert. The possible occurrence of electromagnetic field detection for an insect is discussed with an extensive literature review outlining possible mechanisms.

CHAPTER 1
INTRODUCTION

The cat flea, *Ctenocephalides felis*, is one of the most important pests in the urban environment. Large volumes of research have been devoted to its management, especially around the home. The majority of this research focuses on insecticides, which are the most common means of managing adult flea populations. Behavioral studies on the adult cat flea are rare and often highly anecdotal. Even less has been published on the behavior of cat flea larvae, and virtually nothing has been published concerning their responses to normal and artificial stimuli.

This dissertation investigates a newly found behavior of the cat flea larva, that being its very strong orientation response toward a human being. The behavior was an unexpectedly pleasant discovery that I observed in the laboratory back in 1994. I became intrigued with this behavior and decided to build a research dissertation around it.

Pilot experiments were initiated in order to characterize this behavior and to ascertain what limitations it exhibited. These pilot experiments answered some questions and, as expected, raised some more. Data acquisition was limited to behavioral observations only. A review of the pilot experiments is the subject of Chapter 5. Based upon the results of the pilot experiments, a research plan was devised that included the number of larvae to use in an experiment, the age of the larvae, and the time limit within which all experiments should be conducted. It also became apparent to me that electromagnetic fields may be linked to this behavior, hence, a large part of the experiments and discussion are devoted to this subject.

A simple listing of my results in order to draw obvious conclusions is a procedure I carried out for my Master's degree. Speculating upon the implications of my research, and then probing a wide variety of fields in order to help explain them, is more appropriate for a doctoral level student. The results reported in Chapter 6 are straightforward and relatively easy to follow. However, after the science is reported, the philosophy should begin, after all a Ph.D. is a philosophy degree. Probing questions and the assimilation of literature from all over the world should be, and will be, a primary focus of this dissertation. The most important question to ask is not "What is going on?" but rather "What do I *think* is going on?".

Entomology and electromagnetics are not often found together in the literature. For this reason, a thorough review and analysis of the pertinent literature not only discussing these two areas, but integrating these two areas, is absolutely necessary. The general literature review (Chapter 2) begins with an analysis of insect antennae and their possible role as electromagnetic receivers. This background information will help the reader understand why the antennae of cat flea larvae, as revealed by scanning electron microscopy, could very well be electromagnetic receivers with a high degree of directionality inherent in their structure.

The general literature review will continue with an analysis of insect sensilla, emphasizing their external morphology. Following this is a discussion of basic antennal properties including the effects of antennal arrays, as well as the characteristics of a special type of non-conducting antenna known as a dielectric waveguide. This discussion will tie back in with insect sensilla, thus helping the reader to better understand the link between electromagnetic antennae and insect sensilla.

A review discussing piezoelectric/pyroelectric properties of the insect cuticle relates directly to the detection of various environmental stimuli. This inherent property of insect cuticle will help to explain how stimuli can be received and eventually perceived by an organism without the benefit of distinct sensory organs.

A discussion of the role of antennae in receiving electromagnetic signals would not be complete without a knowledge of the “surface terrain” surrounding an antenna, for this profoundly influences the electrical properties of the antenna and how radiation is received by that antenna. The phenomenon is called “scattering” and volumes of literature have been written about a subject I only wish to introduce to the reader. The presence of spines on the body of flea larvae, their morphological similarity to dielectric antennae, and the odd surface terrains found on flea larval cuticle, especially that region directly surrounding the spines, all strongly suggest an electromagnetic function. The brief review on scattering found in Chapter 2 (entitled “Scatter Surfaces”) will provide the necessary background for the reader to appreciate the importance of scattering and how cat flea larvae may use this physical phenomenon for sensing their environment.

The most comprehensive section of the general literature review will focus on electromagnetic energy due to its large emphasis in the experiments. An overview of the electromagnetic spectrum is an appropriate start, while a consideration of the detection of electromagnetic energy in insects and other animals will follow. These sections will give the reader a taste of the incredible diversity of literature in this field. Many animals show remarkable sensitivities to electromagnetic fields, therefore this section will show that there are "precedents" within Kingdom Animalia. Many studies referred to in this dissertation will be based upon the experiments and insights of scientists who have spent their entire careers studying electromagnetic phenomena and their concomitant effects upon organisms.

The final part of Chapter 2 will focus on specific studies whereby insects respond to individual electric, as well as magnetic, fields. These sections will introduce key points that lead in to the documented occurrence of "biofields" in termites. There are interesting differences, as well as striking similarities between termite biofields and cat flea larval aggregation and orientation behavior.

How magnetic fields are or may be detected by organisms, especially insects, will be the subject of the next section. Because electrical and magnetic fields possess distinct properties, their detection and perception by insects may be just as distinct. It is not likely that magnetic fields are detected exclusively by dielectric waveguides. Instead, research suggests that magnetic fields are probably detected internally and indirectly due to their effects upon physiological systems.

The detection of electromagnetic signals may not only stem from the environment, but from molecules as well. Emissions from airborne molecules originate from molecular bonds that absorb and emit radiation, usually in the infrared, because of vibrations and stretching of bond lengths. The analysis of these molecular emissions helps to identify exactly the molecule in question since each molecule possesses its own infrared "fingerprint". This part of the literature review will introduce and then develop the hypothesis that insects may detect molecular emissions, thus helping them to positively identify a molecule. The possibility that fleas use a similar system will be discussed in Chapter 7.

Chapter 3 is a short review of the literature devoted entirely to fleas, the subject of my research. It begins with a discussion of the ecology of fleas with an emphasis on larval habitat and feeding strategies. Following this will be a specific review of the cat flea showing its dependence upon the host for its survival. The focus of this section will strive to emphasize how vital it is for the cat flea immatures to obtain a blood meal and how this may relate to host detection. This last point leads directly into my dissertation research, and why cat flea larvae may be homing in to such an unnatural host as a human stimulus.

The experimental results appear in Chapter 6, while the discussion section constitutes Chapter 7.

CHAPTER 2
LITERATURE REVIEW 1- GENERAL

Insect Antennae: an Overview

> If the doors of perception were cleansed everything would appear to man as it is, infinite. For man has closed himself up till he sees all things through narrow chinks of his cavern."
>
> -William Blake

Many entomology textbooks place an enormous emphasis on airborne molecules and their role in influencing insect behavior over great distances. Giant saturniid moths were the subject of popular stories because of the documented cases, repeated perhaps thousands of times by amateurs the world over, in which one caged female would release a sex pheromone and thus attract hundreds of potential male suitors (Fabre, 1913). Because research suggests that the ability to detect these molecules is intimately tied to proper functioning of the antennae, antennal morphology is worthy of close examination.

If the molecules adhered to a surface, any surface, then the greater the surface area of the antenna, the greater the probability that a molecule will selectively adhere to it. The bipectinate antennae of the saturniid moths do admittedly exhibit an enormous surface area increase over more filiform type antennae (compare Figs. 2-1a,b with Fig. 2-2a). However, the differences in antennal shape and the size and spacing of olfactory hairs do not appear to affect the deposition velocity significantly (Mankin and Mayer,

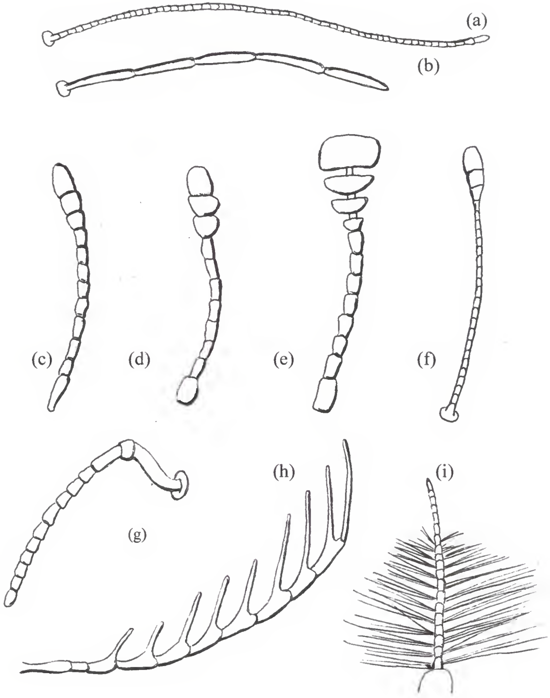

Figure 2-1. Diversity of insect antennae (redrawn from various sources). (a) filiform, Blattodea; (b) filiform, Hemiptera; (c-e) capitate (clubbed), Coleoptera; (f) capitate, Lepidoptera; (g) geniculate (elbowed), Hymenoptera; (h) pectinate, Coleoptera: Pyrochroidae; (i) plumose, Diptera: Culicidae.

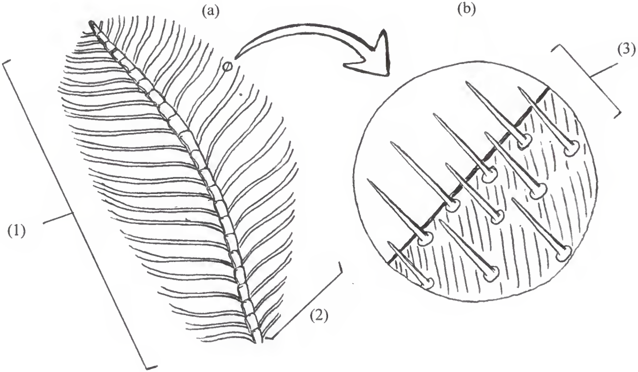

Figure 2-2. Bipectinate antenna of *Hyalophora cecropia* (Lepidoptera: Saturniidae). (a) full antenna [redrawn from cover photograph of the Journal of Applied Optics, Vol. 7]; (b) close-up of trichoid sensillae. (1) first level of proposed electromagnetic detection, the stalk; (2) second level, the branching hairs; (3) third level, the sensillae.

1984). If molecules do not adhere at different rates according to the shape of a given antenna, then how does one explain the various antennal shapes pictured in Figure 2-1?

Insects have survived with very large antennae, such as Cerambycid beetles who may have antennae several centimeters long; or very small antennae, such as the tiny *Trichogramma* parasitic wasps whose antennae can only be seen with the aid of a microscope. The calliphorid fly, *Chrysomya rufifacies*, has been found to be attracted to a cadaver in less than 10 minutes (Byrd, pers. comm.[1]), even though their antennae are small in relation to other insects (Figure 2-3) and contain only a small hair called an "arista" after which the antenna is named. The role of antennal surface area for assisting the insect in detecting airborne molecules was an argument that carried little weight.

A second glance at all of the antennal types shown in Figure 2-1, reveals that most of them look like poor 'molecular nets', in the sense of capturing airborne molecules from the atmosphere, if indeed that is their main function. If antennae have one function, to capture airborne molecules, they should all look relatively the same, because this common function would bind them morphologically. However, insects do not all possess the same morphological type of antennae. Therefore, one may speculate that there are varying functions attributed to each, and if so, these alternate functions should help dictate the final shape of the antenna.

---

[1] Jason Byrd, graduate student in forensic entomology at the University of Florida, personal conversation dated October 1, 1997.

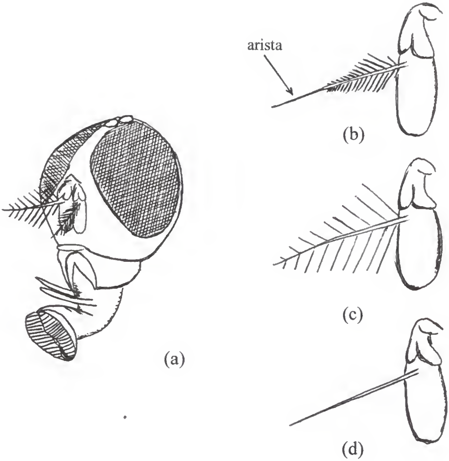

Figure 2-3. Aristate antennae (Diptera) (a) head of Calliphorid fly showing size of antennae relative to head [redrawn from Eickwort, 1984](b) Sarcophagidae; (c) Calliphoridae (d) Tachinidae.

Insect Antennae as Possible Electromagnetic Receivers

The suggested receiver for electromagnetic radiation is commonly held to be the insect's antennae (Laithwaite, 1960; Callahan, 1967; Corbière-Tichané, 1971, 1974; Corbière-Tichané and Bermond, 1972). Much like the former chemosensory hypothesis, so prevalent in entomological circles, this one is absolutely dependent upon antennal morphology, but it views the antennae as morphological structures for tuning in to certain frequencies, and not as an atmospheric "net" for capturing molecules from the air. Laithwaite (1960) calculated that the moth *Orgyia antiqua* has functioning electromagnetic antennae that, due to the spacing of the pectinations, responded to wavelengths between 20 and 200 μm.

Electromagnetic antennal science is extremely complicated. If one wishes to pursue the reasons why some electromagnetic antennae work better than others, a comprehensive background in calculus is required. Even simple layman's terms, as spelled out in an introductory book for radio amateurs (The ARRL Antenna Book, 1974), left my head spinning at times. Therefore, these complex reasons will not be mathematically discussed in this dissertation. What can and will be discussed is the theory behind antennas, which is wonderfully discussed in Kiely's 1953 book entitled "Dielectric Aerials". The saturniid male antenna displayed in Fig. 2-3a takes on a very different viewpoint after reading these two books as well as other books discussing electromagnetic receivers. For example, there are three "levels" of detection for this type of antenna based on only the most fundamental antennal rules.

The first level focuses on the main stalk as an electromagnetic (EM) receiver. The second focuses on the individual hairs stemming from the stalk as EM receivers. The third reduces to the level of the sensillum on those individual hairs (all levels displayed in Figure 2-2). A successful argument may even be made for a more complicated fourth level, that being the successful integration of two or more of these levels.

If the length of the stalk of the antennae itself were 1 cm, then the stalk would resonate when exposed to an EM frequency with a wavelength of 1 cm. It may also resonate to frequencies of 2, 3, 4, 5, or even 6 cm since antennae commonly pick up multiples of the primary frequency. For the same reason, wavelengths ½, 1/3, 1/4, 1/5, and 1/6 would work reasonably well. The U.S. Navy communicated with its submarines with an antenna perfectly tuned to only 1/10 of the communicating frequency (Smith, 1989).

The individual hairs also exhibit similar properties as antennae for the reasons stated above. However, as illustrated in Figures 2-1h,i, 2-2a, and 2-3b,c, the hairs are not all of the same length, but taper gradually so that they closely resemble a man-made log-periodic antennae as shown in Figure 2-4. These antennae are receptive to a general range within the confines of their respective lengths. These man-made log-periodic antennae were the antennae of choice in the 1960's and 1970's, and were positioned on the roofs of houses for improving television reception. The metal rods of these antennae were receptive to wavelengths over a broad range and tapered much like the moth's antennae. Man has since improved upon this now "primitive" practice and uses the radar dish, or "satellite dish" as it is often referred to.

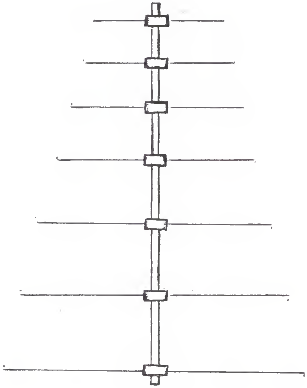

Figure 2-4. Man-made log-periodic dipole array.

The radar dish type of antenna is based on a single detector at the focus of a reflecting dish. The reflecting dish only reflects incoming radiation to the central detector and does not receive the radiation directly. The distance between the dish and the receiver influences the receiving frequencies. Many man-made antennae are constructed with a central receiver surrounded by reflectors or "modifiers" that serve to enhance the antennal properties of the central receiver. The modifiers do this by altering the radiation pattern (The ARRL Antenna Book, 1974) of the central antenna, and are most effective relatively close to this centralized receiver. Figure 2-5d shows a sensillum coeloconica on a grasshopper. This particular form has a central receiver surrounded by a resonant cavity. All sensilla coeloconica have a make-up similar to that briefly mentioned in the paragraph above. Usually they constitute a central peg surrounded by six or more inwardly slanted structures. On the red-banded leaf roller moth about 14 can be counted while on the tiny green peach aphid, an incredible 30 or so can be seen (Callahan, 1975b). A similar configuration is shown in Figures 2-5e,f, the difference being the number of "central" receivers within the resonant cavity. Figure 2-5e is a redrawing of the infrared receptor of *Melanophila acuminata*. The sides of the pit containing the sensory organs are lined with exocuticle (Evans, 1966b) which is highly reflective to light (Callahan, 1990). The sensory organs are, as one might anticipate, not covered with exocuticle (Evans, 1966b) since that might defeat its purpose of sensory perception. These sensory organs are approximately 15 μm long, which is in the infrared range. Still another example is the interommatidial hair of the corn earworm which finds itself surrounded at

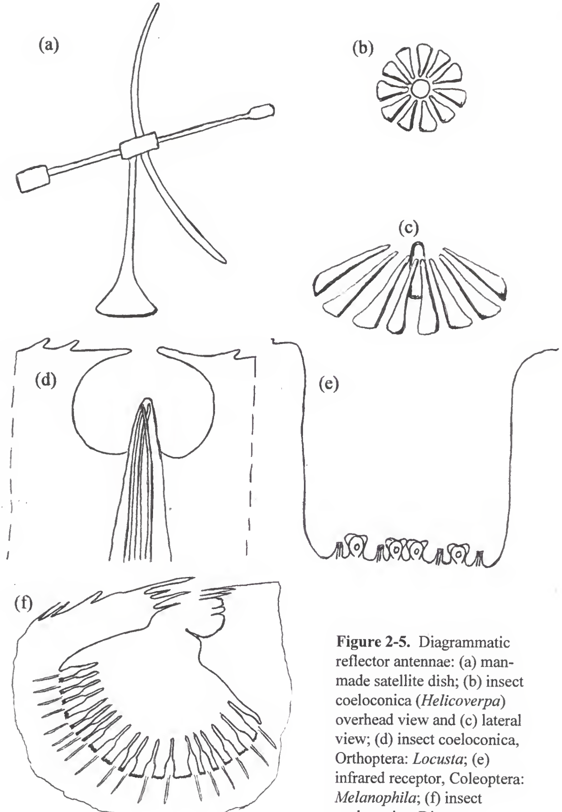

Figure 2-5. Diagrammatic reflector antennae: (a) man-made satellite dish; (b) insect coeloconica (*Helicoverpa*) overhead view and (c) lateral view; (d) insect coeloconica, Orthoptera: *Locusta*; (e) infrared receptor, Coleoptera: *Melanophila*; (f) insect coeloconica, Diptera: *Sarcophaga.*

the base by small stub-like projections (Hsiao and Süsskind, 1970). The difference is that, in this configuration, the modifiers are much smaller than the central peg.

There are, additionally, two good examples of man-made antennae that find analogies in insect sensilla. These are the car antennae and the "rabbit-ear" antennae of old.

The radio antenna found on many cars consists of an elongated metal rod with a spherical metal cap at the end tip. The purpose of this tiny sphere is, in part, to minimize impedance of the incoming radio wave with the antennae. A square or similarly highly angular shape would not work as efficiently. The fact that many insects do indeed possess this characteristic, even across many unrelated taxa, suggests a common purpose. Is this similarity man-made antennae have to insect sensilla a coincidence?

I will ask the reader to refer to Figs. 2-1c and 2-1f and notice the enlargement of the antennal segments as they reach the tip. Two more drawings depict the same phenomenon (Figs. 2-1d,e). Even the lamellate antenna shown in Fig. 2-6 exhibits a form of capitate antennae. Scarab beetles are the only representatives with lamellate antennae and amazingly, all of them have it (it is the distinguishing characteristic).

There are two ways to minimize impedance to an incoming EM wave, the first is by a circular tip (already mentioned) and the second is by tapering the tip. I have often noticed that many scarabs have the three terminal segments of the antennae closed as in Figure 2-6a. The tip will be slightly pointed and round. However, when they bring their antennae out from under their body in order to test the air, the three segments open up as

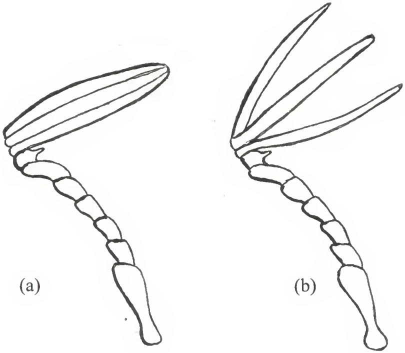

Figure 2-6. Lamellate antennae (Coleoptera: Scarabaeidae) (a) closed; (b) open.

displayed in Figure 2-6b, in fact I have witnessed them opening these terminal segments even wider than the figure portrays.

By performing this action, the beetle has slightly altered the properties of its antenna, at least in terms of electromagnetic reception. There are now three potential receiving sites that are each different from the original tip because of its change in form (a change in form of an antenna always brings about a change in the EM properties of the antenna). An argument can be made that by separating these three terminal segments, the surface area is increased for diffusion of airborne molecules, and that this is the real reason for this behavior. However, if surface area were important to the scarab beetle, they (or at least some) would have the entire antenna shaped like the terminal three segments, and the antenna would then be termed 'pectinate' (Fig. 2-1h). Since this is not the case, one must assume that scarab beetles have this type of antenna for a very, very, good reason. Researchers have already suggested that the lamellate organs on some beetles may be infrared receptors (Corbière-Tichanè, 1971, 1974; Corbière-Tichanè and Bermond, 1972).

The rabbit-ear type of antenna was used for television reception inside the home before cable moved in and erased the need. These antennae are characterized by two rods that can be separated from one another in varying degrees to optimize reception. Once establishing this critical distance, the individual may then revolve the entire apparatus in an effort to increase the quality of reception even further.

Insects also have two antennae composed of two largely hollow rods (Chapman, 1982). They often separate them from one another while apparently scanning the environment. I have often observed insects rotating their own antennae while scanning the environment and simultaneously rotating their entire body. These motions by insects closely resemble the motions taken by a desperate football fan of the past on Sunday afternoon, trying mightily to tune into the "big game".

Antennal Variety

In this section of the review, I would like to discuss some of the similarities and differences of antennal morphology across insect taxa.

Depending upon where you begin your analysis, your comparison could be highly biased. For example, after examining all butterfly species, one may conclude that there is a high degree of consistency since all butterflies are characterized by their knobbed (capitate) antennae. But their close relatives the moths, exhibit pectinate, bipectinate, or filiform antennae. The fact that moths are largely nocturnal is not a valid argument for the difference in antennal shape since a well-known diurnal moth, *Ctenucha virginica*, has pectinate antennae identical to those of its moth relatives.

Similarly, all the true bugs (Hemiptera) have 4 or 5 segmented filiform antennae, but huge variation exists within beetle species (Order Coleoptera). Even though most beetles have either filiform or capitate antennae, all scarab beetles have their own unique form as discussed previously. Ptilodactylids and Pyrochroids (Fig. 2-1h) are both recognized for their unusual-looking antennae which in the latter can be pectinate, serrate, or even plumose in some males.

This last point brings up another difficulty in trying to make sense of antennae, for some beetle species exhibit sexually dimorphic antennal morphology. This is also true of the mosquitoes and midges (Order Diptera) in which the males possess highly plumose antennae but those of the females are relatively reduced. Because both males and females inhabit similar niches one may hypothesize that the antennae for these dimorphic taxa are not modified for the environment but may exhibit modifications designed more for courtship purposes. Indeed, this is suspected to be the case in mosquitoes, where the male possesses plumose antennae designed to tune in to the wingbeat frequency of the female (Fig. 2-1i) (Boo and Richards, 1975).

If one views the antennae of Cerambycid beetles as potential detectors of EM radiation, then the antennal length should be proportional to the wavelength received, or a multiple of the wavelength. Because the antennae are so long (several centimeters or longer) the wavelengths received must be in the microwave region. The sensilla on the antennae would be expected to respond to wavelengths corresponding to their own dimensions, that is, in the infrared and at the 'third level' as discussed earlier and displayed in Figure 2-2. However, the antennae proper would be poor detectors of infrared energy due to their size, and so they must be responsive to longer wavelengths.

The uncharacteristic length of the antennae in Cerambycids appears unwieldy and a hindrance to movement. Therefore, we must assume that these extremely long antennae are in some way necessary for survival since they have been retained in the lineage for so long.

Insect Sensilla, an Overview

Insects have a wide diversity of sensilla located on their body, legs, wings, and most especially, their antennae. Much like my former discussion, prevailing belief among entomologists maintains that these sensilla somehow capture airborne molecules. Chemosensing in insect cuticular sensilla is thought to include:

a) trapping stimulus molecules from solution or air;

b) conducting the molecules through the cuticle to the site of recognition;

c) stimulus recognition with membrane depolarization (generator potential); and

d) generation and conduction of nerve impulses (Zacharuk, 1980).

Chemical recognition in insect sensilla is "assumed" to take place on the plasma membrane of the dendritic terminations.

Common sense dictates some other function as well, since over 400 different shapes and sizes of sensilla exist (Callahan, 1975a). How do these different shapes and sizes enable the sensilla to trap airborne molecules?

> If sensilla shapes do not indicate resonance then exactly what is their function? One cannot isolate them from the system, ignore form and explain all of olfaction by analyzing nerve impulses at the base of the sensilla as is presently done. Nor do nerve impulses recorded from sensilla bombarded with scent explain how the energy from the scent couples to the sensilla, yet to this very day the function of the kinds of shapes of the sensilla are totally ignored... (Callahan, 1990, p. 244)

This incredible diversity in sensillar shape has inspired researchers to categorize insect sensilla. Because the following categorization is relatively recent, I will adopt the system by Zacharuk and Shields (1991) who listed ten categories.

1. *sensilla chaetica*- heavy, thick-walled bristles or spines that are aporous or uniporous
2. *sensilla trichodea*- hairs that may be aporous, uniporous, or multiporous
3. *sensilla basiconica*- peg-like
4. *sensilla coeloconica*- pegs set in shallow pits. usu. aporous, multiporous
5. *sensilla ampullacea*- pegs in deep pits
6. *sensilla campaniformia*- aporous domes within multiporous cuticle
7. *sensilla placodea*- plates level with the cuticular surface. usu. uniporous, multiporous
8. *sensilla styloconica*- pegs set on an elongated style. mostly uniporous, occas. aporous
9. *sensilla scolopalia*- subcuticular
10. *sensilla squamiformia*- scale-like (not found in immatures)

Other sensilla are considered to be variants of these ten basic types, or may even represent a composite. For example, many sensilla trichodea are terraced or possess vertical or helical striations on their exterior. They may also bend or curve toward the tip.

Sensilla can also be categorized by virtue of their electrophysiological function into mechanoreceptors, chemoreceptors, or photoreceptors. It should be emphasized that neither the modality nor the specificity of a hair type can be predicted from its appearance under the light microscope (Hansen, 1978), however, some generalizations can be made and do help to simplify an otherwise difficult issue.

"Mechanoreception is the perception of mechanical distortion of the body caused by the external stimuli of touch and air- or water-borne vibration, or due to the internal forces generated by activities of the muscles." (McIver, 1975). Mechanoreceptors consist of one or two dendrites that innervate the base of the sensillum (Thurm, 1964).

Chemoreceptors are characterized by their response to olfactory stimulation, and morphologically as sensilla with multiple dendritic innervations. If they are thick-walled and possess a single opening at the tip they are considered to be gustatory chemoreceptors

(Dethier, 1963; Slifer, 1970); if thinner-walled, and possessing multiple pores then they are considered to be olfactory chemoreceptors (Slifer, 1970; Zacharuk, 1980). Usually the sensillar tip has a terminal pore with a dendrite directly beneath it. However, some sensilla do not have that terminal pore seemingly disqualifying them as contact chemoreceptors except that a dendrite is still encountered less than one micron below the tip. A mechanoreceptor has no terminal pore, or any pores in its cuticle, but the dendrite terminates at the base of the sensillum and does not extend to the tip.

Behaviorally, this classification may not stand up either, since a contact chemoreceptor discovered by Städler and Hanson in 1975 was found to have "olfactory" capabilities. Similarly, the efficiency of the grooved-peg sensillum on *Aedes aegypti* as an olfactory receptor does not appear to be affected by the fact that is has only a single terminal pore (Davis, 1988). Städler and Hanson (1975) have commented that this convenient separation of all chemoreceptive sensilla into one of two groups does not always apply. They cited behavioral support from Slifer (1970) and the physiological study of Dethier (1972) along with their own electrophysiological results. In addition, the presence of both contact and olfactory sensilla on the same organs (Dethier and Kuch, 1971) means their location can not be a criterion for classification either. If this classification scheme is not very reliable, then its use should be curtailed.

The difference between mechanoreceptors and chemoreceptors is often inferred from their internal morphology and may be just as difficult to separate reliably. Often, an individual sensillum exhibits a dual function, that is, both mechano- and chemoreceptive functions. These chemo-mechanosensory sensilla were positively identified on ticks

(Foelix and Axtell, 1971; Foelix and Chu-Wang, 1972; Chu-Wang and Axtell, 1973) as well as beetles (White and Luke, 1986) and moths (Callahan, 1968) and are discussed in a review article by Zacharuk in 1985.

White and Luke (1986) found that non-porous hairs that tapered to a fine point were the most common type on the antennae of a beetle, *Oryzaephilus surinamensis*. Since these sensilla are the most common, and they have no pores, just how is the receiving molecule internalized by the antennal sensilla for eventual detection by dendrites if chemosensory function is supposed? Additionally, some sensilla with a slit opening had an innervated dendrite just below the slit, while others did not. Because detection of molecules is thought to be dependent upon dendritic stimulation by the airborne molecule, why were there no dendrites underneath some of these openings/slits? Diffusion would take far too long to pass down the entire length of the sensillum. If the sensilla does not allow molecules to pass through its impermeable cuticle, then what indeed is its function? Why are these pores found in so many different shapes and sizes as represented in the insect world? Three differently shaped porous sensilla were even found to exist on a single insect, *Cimex lectularis* (Steinbrecht and Müller, 1976) Could all of this be simply attributed to random variation, or could there be an underlying function?

Some of these tapered hairs became abruptly blunt and occasionally swollen at the tip just as a clubbed antenna or a capitate antenna would be. No hypotheses in the literature have been found speculating how this morphological adaptation increased the capture rate or ability to capture an airborne molecule. Pilgrim (1991a) reflected on this phenomena while admiring these sensilla on flea larvae when he asserted that "...at least those with swollen tips *must* have a functional significance" (italics mine).

Insect antennae are generally considered to be chemoreceptive organs consisting of a plethora of chemoreceptors. Why then is it that 68% of the antennal sensilla of *O. surinamensis* are mechanoreceptors (White and Luke, 1986)?

Clearly, many incongruities exist within the present classification scheme. At least 400 different types of sensilla (Callahan, 1975a) exist on insects and contemporary entomologists contort this variety into only three functional types. Is it even remotely possible that various insect sensilla are resonators for electromagnetic frequencies as several researchers have suggested over the years (Grant, 1948; Miles and Beck, 1949; Laithwaite, 1960; Callahan, 1967)? To investigate this possibility further, I will first discuss some of the basic properties of an antenna, insofar as they relate to insects.

Antennae Fundamentals

A dielectric waveguide is a type of antenna. However, it differs from a traditional antenna primarily in the material of which it is composed. Traditional antennae are made of a conducting substance, such as metal, but dielectric antennae are not. They may be composed of almost any material that is a poor conductor.

The prefix 'di' means 'two' and refers to the two electric charges found on opposite sides of the non-conducting material. The reason for this charge separation is due to the dielectric material, which because it is a non-conductor, prevents the dissipation of charge to cross from one side to the other. Generally, the adjacent sides contain opposite charges, one positive, the other negative (Athenstaedt and Claussen, 1981).

Fortunately, the two antennae types have similar functions, which will make this section easier for the reader to follow. Basically, a given wavelength or frequency can be received by both types of antennae. In some instances, however, one antenna will have an advantage over the other, but both will work under most conditions. For this reason, I will first review selected properties of a standard antenna, and will then follow with basic dielectric waveguide theory, and then finally I will conclude with the striking similarities that are found between dielectric waveguides and insect sensilla.

Exact theories for antennas are not usually available or even understandable because of the complex equations and higher level calculus that is involved in predicting their properties. Therefore, antenna research began empirically with the construction of various materials into many different shapes and sizes in order to determine experimentally what worked and what did not. The first man-made electromagnetic antenna was developed by Hertz in 1887 and was, quite simply, a circular loop of wire. The results obtained from this and subsequent studies have revealed four fundamental properties of all antennas. In order to help me recall these properties, I have labeled them with the acronym "G.R.I.P." They are gain, radiation pattern, impedance, and polarization.

The *gain* of an antenna is the ratio of the maximum radiation intensity to the maximum from a reference antenna with the same power. Measurement of gain is accomplished by direct comparison with a calibrated standard-gain antenna which is specifically designed for a particular frequency (The ARRL Antenna Book, 1974). Therefore, a given antenna with an established gain will be found to have its gain altered when different frequencies are tested. Gain in one direction is always obtained at the expense of gain in other directions. High gain in the direction of the signal both lessens the requirement for later amplification and reduces the noise picked up in directions from which signal does not arrive. Gain is closely related to the directivity[2] of an antenna and books will often use these terms synonymously[3], a usage I will adopt for this paper.

The *radiation pattern* of an antenna determines the spatial distribution of these radiation intensities. It refers not only to the maximum radiation intensity, usually in the form of a lobe, but also to all secondary lobes (Figure 2-7). Determining the radiation pattern is important because large secondary lobes decrease the gain of the antenna, and knowing they exist in a given pattern allows for various adjustments to be made so that reception is optimized. The two main features of a highly directive radiation pattern, and therefore a highly directive antenna, are narrow beamwidths[4] and small sidelobe levels (Figure 2-7b).

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[2] All antennas exhibit directivity because the intensity of radiation is not the same in all directions.

[3] Directivity is based solely on the shape of the directive pattern, but gain takes into account power losses which adjust the lobe pattern.

[4] Beamwidth of a directive antenna is the width, in degrees, of the major lobe between the two directions at which the relative radiated power is equal to one half its value at the peak of the lobe.

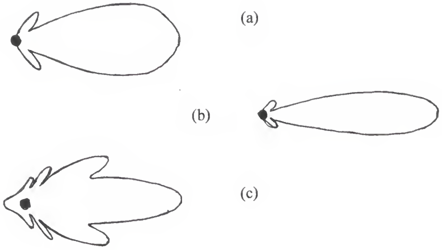

Figure 2-7. Three types of directive radiation patterns for hypothetical antennas. a) directive pattern with main lobe and two secondary (2°) lobes; b) highly directive radiation pattern with reduced 2° lobes; c) directive radiation pattern with disruptive 2° lobes

Impedance is the property which allows for the incoming frequency to be detected from the atmosphere without loss. This property is presented by the antenna at its terminals, and provides a smooth transition and a certain degree of matching with the atmosphere.

Polarization is usually defined in terms of the orientation of the radiated electric field "E" in the direction of maximum radiation (i.e. a vertical wire antenna is vertically polarized). Antenna polarization is generally elliptical. One final characteristic of antennas is given its own theorem. This is known as the Reciprocity theorem, which states that the properties of antennae (G.R.I.P.) are the same for both transmitting and receiving. Therefore, if insect sensilla are antennae, their intrinsic ability to send electromagnetic signals is equivalent to their ability to receive signals from the environment. This fact has enormous implications for intraspecific as well as interspecific communication among insects, most especially among social insects (i.e. ants, bees, and termites).

Antennae are a vital part of many communication and radar systems, and are usually an important topic in final year undergraduate courses and M.Sc. courses in electronic engineering. They are the basic components of any electronic system which depends upon free space as a propagation medium. Antenna dimensions can vary from very small fractions of a wavelength to many wavelengths. This suggests, correctly, that antennas assume very different sizes for different frequency bands. Long-wire antennas are simple both electrically and mechanically, and there are no critical dimensions or adjustments possible. As the wire becomes gradually longer, the width of the main radiation lobe decreases, thus improving the gain and the overall antenna efficiency. For example, the lobe size for a particular antenna at a given wavelength (1λ) was 90° while a similar antenna eight wavelengths long (8λ) displayed a main lobe of only 30°.

For directional antennae, it is desirable to have a narrow beam width and for the radiation to be projected forward in one direction. Although the forward mass of radiation is the main lobe, antennae often exhibit side lobes as well. These side lobes decrease the gain of the antenna, and therefore need to be controlled if possible.

Antennae designed for navigation usually have a narrow beam width, and the radiation is projected forward in one direction. A radar system usually requires a high gain antenna which can be steered to scan over a particular area. Thick-walled antennae work well over relatively wide bands of frequency, while thinner-walled antennae are rather sharp in tuning.

Other antennae need not be directive but only of the appropriate length. I have already mentioned submarines utilizing antennae of appropriate length but airplanes must deal with this problem as well. Aircraft take the length of the plane into account in order to "lengthen" their antennas so as to properly tune in to the correct wavelengths from the ground. Electrically small antennas (length $<< \lambda$) have a very poor radiation efficiency. This is a basic limitation of electrically small antennas. Optimized antennae can be *absolutely* small, but not *relatively* small. One exception to this rule concerns infrared detectors which reportedly improve as the devices are made smaller than the receiving wavelength (Hu and Richards, 1989; Peatman and Crowe, 1990).

Coupling and Arrays

When two similar antennae are brought within a certain critical distance of one another, *coupling* is said to occur. This is no more than interference of the radiation patterns so that a new form is created. More often than not, constructive interference may occur such that the field strength may exceed the field produced by the same power in a single antenna.

Linear arrays consist of three or more antennal elements lined up such that all are contributing to form one unique radiation pattern. Generally speaking, the linear array is more directive than any of its elements alone, so that it dominates properties such as main beamwidth and sidelobe levels; in fact, the radiation pattern of the element is practically lost to the radiation pattern of the array. Assuming no coupling in an array (equidistant elements), the main beamwidth is governed by the complete array length. Certain combinations of antennal elements result in very specific directive patterns. The gain and directivity that can be secured by intentionally combining antenna elements into an array represent a worthwhile improvement both in transmitting and receiving.

Two varieties of linear array include the end-fire array and the broadside array. The principal direction of radiation for an end-fire array is parallel to the axis of the array and to the plane containing the elements while the broadside array has its principal radiation perpendicular to the axis of the array. It is characteristic of broadside arrays that the power gain is proportional to the length of the array but is substantially independent of the number of elements used, provided the optimum element spacing is not exceeded.

Both broadside and end-fire arrays can be readily combined to increase gain and directivity and this is in fact usually done when more than two elements are used in an array. The combinations that can be built are practically endless.

A phenomenon related to coupling is a parasitic array. This differs from true coupling in that one antenna is not powered via external sources. This parasitic element has no power associated with it except for the power it picks up solely from its close proximity to the power element containing the current, known as the "driven element". Parasitic elements not only have their own radiation pattern altered, but they also affect the radiation pattern of the driven element. The actual impedance of an antenna element, becomes the sum of its self-impedance (with no other antennas present) and its mutual impedance with all other antennas in the vicinity. Although the calculation of mutual impedance between antennas is difficult, model antennas show that adding parasitic directors and/or reflectors often increases gain for specific frequencies.

A special type of parasitic array involves parasitic elements acting as directors or reflectors. The driven element is centrally located and is surrounded by parasitic elements that may act either as a director or a reflector depending upon their size and/or location relative to the driven element as well as the phasing of the current(s). This situation is analogous to the sensillum coeloconica of Fig. 2-5c.

Reflector arrays may also take the form of a dish, such as the radar dishes many of us use to pick up satellite transmissions for television broadcasts (Fig. 2-5a). Because reflector antennae are highly directive, they are often revolved in order to receive signals from all directions. Other antennal arrays are modified to receive from all directions but have no directionality (radiation lobes extend out in all directions). This situation is analogous to the sensilla coeloconica represented by Fig. 2-5d.

Since associations into groups, communities, populations, and biocenoses exhibit their own specific features due to "coalition", an aggregate of elements can jointly do things which each of them separately could never achieve (Presman, 1970). The individual units, whether they be of a conducting nature or a dielectric nature, also have their bearing on how an antennal array will function. In insects, sensilla arrays are the norm, not the exception, and are indicative of multiplicative signal processing dielectric antennas.

Dielectric Waveguides

As I have already mentioned in the introduction, dielectric aerials employ a system of dielectric elements, as distinct from a system of conductors, to either radiate or collect electromagnetic energy from one or more directions. The very general properties for antennas mentioned above also apply for dielectric antennae. Because insects are not composed of metal, their antennae are not likely conducting but are probably dielectric. Therefore, some characteristics of dielectrics are discussed below in order to help clarify their role in sensory perception.

The transmission of sinusoidal electromagnetic waves in waveguides was first investigated by Tyndall in the 1860's (Tyndall, 1866) and later developed by Rayleigh in 1897. Although investigators continued to study dielectric waveguides throughout the early part of this century, their practical importance was not realized until some 30 years later (Barrow, 1936; Carson et al., 1936; Schelkunoff. 1937; Chu and Barrow, 1938) and they were first used by the Germans in World War II (Callahan, 1989). The three main types of dielectric aerials include 1) a solid dielectric rod, 2) a hollow dielectric tube, and 3) a dielectric horn. Only the first two will be discussed at any length.

These three radiators may all be excited by conventional methods and they all have the common property that they produce single lobe radiation patterns directed along the axis of the aerials. Their directivity is proportional to their length, which is the most distinctive characteristic of the family. Additionally, the efficiency of dielectric waveguides is such that energy loss from a wave to the waveguide is zero; mathematical and experimental verification of efficient dielectric waveguide systems is well documented (Weinstein, 1969).

Generally speaking, a correctly designed dielectric tube antenna is more directive than a dielectric rod of the same length. Most insect sensilla are not solid cuticle throughout, but instead are tubular. Additional factors that modify an antenna's efficiency include taper, diameter, thickness, dielectric constant, length, and its presence within an array.

Gradually tapering the antenna as well as decreasing the diameter may both severely reduce the side lobes, thus increasing the main lobe and the antenna's gain (Mueller, 1952). Increasing the taper by only a small margin, say from 2° to 4°, was enough to decrease the side lobes noticeably (Callahan, 1985.) Tapering the rod provides impedance matching to free space and minimizes reflection at the end of the rod, thereby producing a field distribution along the length of the rod that results in smaller side lobes. Gradual tapering along the entire length provides for better impedance matching than a more abrupt taper.

The thickness of the antenna is also very important, but optimization is difficult to achieve. The thinner the dielectric tube, the greater the power. However, a very thin antenna will have structural problems or will at least break easily. The only known compromise has been to perforate the antenna with extremely fine pores (Mosely et al., 1964). This simulates an infinitely thin wall, while at the same time does not sacrifice structural integrity. Arthropod chemoreceptors are characterized by their thin walls and very fine pores (Slifer, 1970; Zacharuk, 1980) that can only be seen with the aid of a scanning electron microscope (Foelix and Chu-Wang, 1973). It is entirely possible that the presence of fine pores in a particular sensillum, may exist in order to increase the power of the "antenna", more so than their purported function as simple "windows" for allowing the passage of molecules through an otherwise impermeable cuticle.

In a dielectric antenna, the dielectric constant helps to determine the resonant wavelength of the antenna. Dielectric rod aerials have been made with polystyrene which has a dielectric constant of 2.5. If materials of higher dielectric constant are used, the diameter of the rod must be reduced to give similar performance.

The use of longer dielectric rods helps to systematically reduce the width of the main radiation lobe by a factor of two or more. For example, when the length of a dielectric rod was increased from 2λ, to 4λ, to 6λ, and finally to 8λ, the beamwidth decreased from 57°, to 40°, to 30°, and finally 25°, respectively (Kiely, 1953).

Beamwidths narrower than about 20° cannot be achieved with a single dielectric rod, and it is necessary to use arrays of rods to obtain narrower beams and to enhance performance. Another experiment involving four dielectric rods spaced 3/2 λ apart produced a beamwidth of only 10°. Arrays of two and four dielectric rods were used extensively in Germany during World War II as radar aerials and as search aerials for detecting allied radar transmissions. A large rectangular array of 42 dielectric rods was designed in the United States at Bell Telephone Laboratories and was used by the American Navy for gunnery fire control purposes (reported in Kiely, 1953).

The properties of biological dielectrics have been discussed by Schwan (1957), Grant and co-workers (1978), Pethig (1979), and Hasted (1973), among others. Unfortunately, none of them investigated the dielectric properties of insect cuticle.

Insect Sensilla and Radiation Detection

Charles Valentine Riley, former chief of the Entomological Commission and author of Insect Life (1889-1894) suggested that insects might sense subtle vibrations to which we are blind (Riley, 1894). Jean Henri Fabre (1913) was the next to publish his thoughts that perhaps moths are tuned to certain electromagnetic frequencies, while Eugene Marais (1937) speculated that termites might do the same. Electromagnetic frequencies are, of course, picked up by appropriately structured antennae, but no one looked for them on insects until 1948 when Grant, an electrical engineer, was the first to publish a paper indicating a possible detector for this EM radiation by pointing out that certain pit sensilla on insects closely resembled dielectric waveguides and resonators already developed by man (Grant, 1948). One year later, Miles and Beck (1949) hypothesized that certain olfactory receptors are indeed radiation receptors, based upon their experiments with honeybees and the bees' attraction toward an enclosed box containing honey. This box was equipped with an infrared transparent window. Duane and Tyler (1950) hypothesized that the infrared radiation arising from the body heat of the female moth could be the signal that attracts the male. Laithwaite reopened the subject again in 1960 when he discussed the assembling of moths due to radiation and agreed with Grant by noting the similarity of insect antennae to certain radar antennae designed by man. None of these researchers, however, continued to publish on this subject.

Phil Callahan developed the hypothesis in the 1960's when intensive research began in his laboratory (Callahan, 1965a,b,c,d, 1967, 1968, 1969). Support for this hypothesis came from Griffith and Süsskind (1970) who by creating models discovered that insect sensilla trichodea could very well be working dielectric antennae. Hsiao and Süsskind (1970), Hsiao (1972), and Griffith (1968), suggested that the optimal operating setal length for a dielectric antenna was 6 wavelengths and they all found support for this theory in various forms. Evans (1966b) investigated infrared receptors and infrared radiation from sensory pits on a beetle as Grant (1948) had first pointed out. Okress (1965) added theoretical support for the dielectric waveguide theory for insects, while in a personal communication to Callahan pointed out that dielectric theory was more suitable than conductive theory (reported in Callahan, 1981). Eldumiati and Levengood

(1971) made the observation that the moth's major antennal spines are hollow thin-walled tubes with a tapered cross section. They too concluded that this structure would be suitable as a dielectric antennae.

Many insect sensilla are elongated spines or hairs called sensilla trichodea (meaning hair sensors). These sensilla are not localized to a body region but can be found on every region of some part of some insect's cuticle. They all taper gradually to the tip, which is often quite pointed and which provides very good impedance matching with the atmosphere. The sensilla have very thin walls, much thinner than that found covering the body proper (an excellent picture can be found in Figure 1 from Zacharuk et al., 1977) and of a fixed consistency throughout, resulting in a uniformly sclerotized spine (Richards, 1952). Often these spines are perforated with tiny pores, which electrically reduces the thickness of the cuticle by reducing the dielectric constant and increasing antennal gain, as mentioned earlier. The length of most of these sensilla trichodea are less than a millimeter, which places their optimal frequencies for electromagnetic detection in the infrared range (Callahan, 1965a) or the microwave range (Callahan et al., 1968). Eldumiati and Levengood (1971) suggested that longer wavelengths may be detected if the main trunk is considered as a waveguide.

Based upon the lengths of some sharply tapering spines occurring on the scape and pedicel of several species of noctuid and saturniid moths, these spines may be tuned to the visible region of the spectrum (Callahan et al., 1968). Electrophysiological responses have shown these spines to respond to frequencies across the entire visible spectrum (Callahan, 1968). A correlation between length of sensillar hairs (trichobothria) and frequency perceived was found by Gorner and Andrews (1969) and Drasler (1973). These articles show that different antennal lengths are differentially tuned to various frequencies regardless of whether it be a man-made antenna or an insect antenna.

Since infrared radiation falls between the visible and radio regions of the spectrum, infrared demonstrates many of the characteristics of both. It may be focused by lenses and yet can be transmitted like radar or radio through materials that block visible light. Emphasis is added to this comparison by the use in infrared technology of both optics (refraction and reflection) and radio (waveguide and resonant cavities) techniques to detect such radiation (Valli and Callahan, 1968). The fact that infrared radiation may behave like both can be revealed theoretically and by direct measurements obtained through the making of antenna models. Some unique properties of infrared antennas have been revealed by Hu and Richards in 1989 and Peatman and Crowe in 1990. These two groups found the performance of many types of infrared detectors improve as the devices are made smaller (<< wavelength).

Model insect dielectric antennae were designed and investigated by Callahan (1991) who found that the longer and thinner the sensillum type. the more directional was the associated radiation pattern. Conversely, the shorter, stubbier insect sensilla, corresponding to sensilla chaetica and sensilla basiconica, displayed a broader beam width and therefore a loss in gain. Trichodeae which are curved also have a radiation pattern which reflects this, such that a trichodea curved to the left side will have its major lobe curved to the left as well.

Corrugating a sensillum basiconica increases beamwidth until it is almost totally nondirectional. These sensilla have been found on many insect antenna as well as on the hind legs of mosquitoes. Similar corrugations have been found on the blowfly (Dethier, 1972), the bed bug (Steinbrecht and Müller, 1976), the cerci of a cricket (Schmidt and Gnatzy, 1972). On the sensilla trichodea of honey bee antennae (Dietz and Humphreys, 1971) they appear under the scanning electron micrograph (SEM) as ridges spiraling up the sensilla, barber-shop style. Additionally, the bed bug (Steinbrecht and Müller, 1976) and many other insects have both smooth and ridged sensilla, thus showing that the differences are not species-related.

Wavelengths in the microwave-infrared-visible range cannot penetrate the cuticle to a significant degree (Presman, 1970; König, 1989). The shorter the wavelength the more easily it is absorbed by matter. This means that if electromagnetic bioinformation is to be transmitted between living beings, both the signal source and the receiving site (receptor) must be placed on the surface of the body (König, 1989). The only sensory structures on the outer surface of insects are the sensilla as well as the legs and antennae proper. It seems natural that the insect sensilla would have this purpose of directing and collecting the electromagnetic radiation since this function has already been established for very similar surface structures on the compound eye of insects.

There are protuberances on the insect cornea that Bernhard and Miller (1962) have called “corneal nipples”. These nipples are arranged in a perfect hexagonal array, and this degree of precision strongly points to a very specific function. After making measurements on scaled dielectric models and based upon spectrophotometric analysis on insect corneas, they concluded that this corneal nipple array acts as an impedance transformer which matches the characteristic impedance (inverse of refractive index) of air to that of the lens material over a broad wavelength range (Bernhard et al., 1965). These results were confirmed by the application of a mathematical model.

The insect exoskeleton is composed of a very rigid cuticle known as chitin. Hardened or stiff antennae with good solid walls make better antennae than those with flimsy, pliable walls. The waxy layer covering the insect cuticle also has its role. The waxy layer has a dielectric constant between 2.5 and 3 (Callahan, 1967), which is similar to the dielectric constant of polystyrene, an excellent dielectric. Both Griffith (1968) and Shackelford (1970) also determined that the insect exoskeleton and insect waxes are excellent dielectrics with the proper dielectric constant for a dielectric antenna, thus adding their support to Callahan's hypothesis.

Many biological epithelia are provided with a waxy protective layer which apparently developed as a necessary prerequisite for an organism moving from an aquatic to a terrestrial existence. The wax layer can also have the structure of a permanent electrical dipole conforming to the physical laws of an electret (Warnke, 1989a). An electret is any insulator containing a stored charge (Mankin, 1976) . Electrets can be formed by different methods, such as in the presence of heat or an electric field. Liquid beeswax exposed to an electric field will also harden into an electret (Jaeger, 1934) as does carnauba wax when exposed to a magnetic field (Bhatnagar, 1964). A drop of purified beeswax, filtered through filter paper, and diluted with benzene, still did not form an even layer when applied to a flat plate (Mankin, 1976), whereas the wax layer apparently forms an even coating on each spine of an insect from molt to molt.

Piezoelectric and Pyroelectric Properties of Insect Cuticle

The ability of any insect to detect external stimuli is largely dependent on the properties of its cuticle. I have already mentioned the sensilla and the evidence supporting their possible function as working electromagnetic antennae. However, not all antennae are passive detectors of electromagnetic frequencies. Usually, their primary function is to "...pick up (lock into), amplify, and in the case of arrays, analyze a signal." (Callahan, 1973). This brings us to a very important question; what is the detector or at what level does detection take place?

Beament (1961) measured a potential difference of 2 x 10^4 V/cm across the cockroach integument. The resistance found across the insect cuticle was measured at 10^8 Ω by French (1988). Measurements with both living and dead flies demonstrated voltages between parts of the body (Becker and Speck, 1964). The voltage source was hypothesized as originating from a galvanic element which consists of the protein of the body and the cuticula. This "body battery" as Becker and Speck named it, could be switched off by complete drying only to set in once again when moistened (Becker and Speck, 1964).

The very high resistance found across the insect's cuticle helps to explain the dielectric properties of the cuticle, whereby a very effective charge separation can be maintained. This property of the cuticle also confers upon it a certain degree of mechanical stress, extremely sensitive to impinging vibrations. Piezoelectricity is the property of a substance such that it converts pressure to electricity or electric polarity. Pyroelectricity has a similar definition but substitutes heat for pressure. Any structure with piezoelectric activity also has pyroelectric activity (Warnke, 1989a). For most dielectric materials, the polarization disappears when the field is removed. In some crystals such as triglycine sulfate (TGS), however, a strong residual polarization remains. The residual polarization of pyroelectrics is strongly sensitive to minute changes in temperature. If temperature is varied, even in the slightest degree, the consequent change in residual polarization causes a new charge to appear across the dielectric. The charge will be positive or negative depending on the direction of the temperature change (Callahan and Lee, 1974).

Piezoelectric properties of the insect cuticle were first reported by Callahan (1967). He found that the exoskeleton produced both sound and radio waves when stressed. That same year Morris and Kittleman (1967) found piezoelectric activity in the otoliths of some species of bony fishes, where it is believed to be involved in sensory perception. Six years later, Strickler and Bal (1973) suggested that the microtubules may connect the sensory neurons with the moving tip of the hair (sensilla) and function as a piezoelectric crystal. The topic developed nicely with the work of Zilberstein, Athenstaedt and colleagues who measured both piezoelectric and pyroelectric (PZE and PE) properties of the cuticle not only of insects, but some other arthropods as well.

It was discovered that PE and PZE responses will not only occur in live insects (Simhony and Athensteadt, 1980) but will also be measurable in dead, dry integument preparations as long as the polar tissue texture remains intact (Athenstaedt and Claussen, 1981). Although it is true that the PE and PZE voltage responses of the integument of live animals were considerably higher than those of the same animals after death, the post mortem responses declined steadily for about three hours (without changing the position of the specimen) and then remained constant over a period of months (Athenstaedt and Claussen, 1981). Athenstaedt (1972) found that PE and PZE properties were found to exist in the integument of beetles that have been kept in zoological museums for more than ten years. The natural conclusion to be drawn is that the established PE and PZE effects are due to a physical "material property" of the integument and that they are not caused by ionic transport or other bioelectrical phenomena normally associated with the living state (Athenstaedt and Claussen, 1981) However, since these properties can be enhanced by the living state, it might be that the insect augments this property for heightened sensory detection. Due to its polar texture, the insect integument will react to rapid changes in temperature, illumination, or uniaxial pressure in the same way as nonbiological PE materials. It seems entirely possible, therefore, that the well-known physiological reactions of various arthropods to such physical outside influences may be related to the PE property of their integument (Athenstaedt and Claussen, 1981.)

A hard, relatively stiff material is a prerequisite for PE and PZE activity. The mechanism of mollusc shell formation involving material deposition under the influence of a steady polarizing field generated by the periostracum is very similar to the processes used in industry to polarize piezoelectric ceramics and other materials (Zilberstein, 1972). Since PZE activity is found in insects as well, one may entertain the possibility that insect cuticle is formed under a polarizing field (during molting) just as the shell is in molluscs.

Standing waves in a mollusc shell (*Limulus* sp.) bounce back and forth within the structure, generating a voltage whenever they impinge on the electrodes (Zilberstein, 1972). When the shell is placed in a damping medium, such as water, only the initial response is observed. The natural state for many mollusks is in the water and this response points toward an obvious sensory function especially in those molluscs which seem to perceive sound despite the apparent absence of any recognizable sensory organ.

Sense organs for many electromagnetic frequencies have not been found in insects, although several studies have shown that insects respond to these same frequencies. It is worth repeating that the EM frequencies in question are not capable of penetrating the insect cuticle to any degree (Presman, 1970). The depth of penetration of EM waves into various tissues decreases with increasing wavelength. Therefore, one may conclude that since the insects detect these wavelengths and since they cannot penetrate the cuticle, the receptors cannot possibly be inside the insect, but instead must be located on the outside of the insect. The countless sensilla found on the insect's cuticle are the primary candidate for external receptors. A general function of antennae is to amplify the incoming message. These sensilla may be detecting and amplifying low levels of energy in the external environment that would otherwise be undetectable to insects. It is known that organisms are sensitive to static fields and to EM fields of various frequency ranges several orders of magnitude lower than the theoretically predicted value (Presman, 1970).

If organisms can detect EM energy below background (noise) levels, then they could be transmitting/detecting coherently. For example, although the power of acupuncture lasers is low (only 2-5 mW) its spectral intensity is much larger than that of sunlight (Kroy, 1989). Since all parts of the optic wave are in the same phase-rhythm, correlated multiphoton effects such as interference-structures occur, making coherent messages more complicated and therefore, increasing the amount of information transmitted.

Fritz-Albert Popp (1989) has shown repeatedly that organisms transmit and receive coherently, and a waveguide or resonator will tend to pick out coherent signals from a noisy background (Diesendorf et al., 1974). Additionally, coherent oscillations are able to perturb bio-communication systems, only by small amounts when the system is under good homeostatic control, but by appreciable amounts when the system is under biological stress (Smith, 1989). This means that a given organism may not be equally sensitive to a particular radiation from one day to the next or even from one moment to the next.

Dielectric Antennae: Possible Function in Insects

Critics have maintained that electrophysiological techniques should be employed to determine whether a particular sensillum resonates to a particular EM frequency

(Diesendorf et al., 1974). One problem with this approach is that a dielectric system is dependent upon a charge separation that must be maintained. Conductivity can be adversely affected, or assisted, by the presence of pore canals or glands (Mankin, 1976). Any leakage, such as a large hole caused from an improperly placed electrode, would necessarily disrupt the system the researcher was trying to measure. The neuron might still respond, but the system that regulates when that neuron fires would be compromised. A negative result might then be misconstrued, and a positive result could not be reliably understood to be a positive response.

Furthermore, the presence of a neuron or neurons, in the sensillum is not an indication that they detect and/or transmit a neuronal spike in response to an EM frequency. Instead, their presence may be only to increase the power of the sensillum, which acts as an antenna. In other words, they would be driven elements. The increase in power could result in an increase in gain, thus rendering the antenna (sensilla) more directive.

There is the possibility however, that the insect detects radiation by means of an antennal array. If this is the case, then the array should be examined and not the individual elements. But how would one go about testing this possibility? An array could be linked together directly beneath the cuticle. The sensilla responding to the EM frequency would resonate thus vibrating the cuticle due to their close association. The sensilla would then be viewed as collectors, and the underlying sclerite as the detector. A neuron, or several, need only associate with the cuticle and not the sensillum directly. If this situation were occurring, then the researcher's approach should focus on locating the neurons (dendrites) that innervate the cuticle.

Evidence supporting this hypothesis can be found on the cabbage moth larva, *Barathra brassicae*. This caterpillar responds to low frequency sound stimuli with defensive reactions (stopping, squirming, dropping). Minnich (1925, 1936) experimented with tuning forks and the responses of various caterpillars and found sensitivities in the 30 to 1000 Hz range which is within the wingbeat frequency of all insects. The medium vibration in the near-field (up to 70 cm) of a flying wasp is an adequate stimulus for the hair as calculated by Tautz (1978). Eight filiform hairs mediate the sound sensitivity, but only four hairs are necessary for a normal sound reception threshold response (Markl and Tautz, 1975). Only two intact hairs revealed that the threshold response increased threefold, and with only one hair, the threshold response increased sixfold. This condition cannot occur without some degree of interaction/communication between the 8 hairs.

This set-up has already been copied by man. The U.S. Department of Defense has long known this since government documents were declassified back in the 70's showing infrared sensors based upon the morphology of insect sensilla. The "spines" were non-innervated tungsten detectors that were only 15 μm in length and 2-3 μm in width (Callahan, 1977b, p. 116) or 5-10 μm long and situated in pits (Callahan, 1977b, p. 117). These man-made sensilla are all attached at the base to a uranium dioxide plate and the apparatus, called a "Thermal image projector-recorder", is used for infrared detection (Redman, 1974). Much more recently, however, technology has progressed to where we may now etch "microlasers" (Jewell et al., 1991) on plates that closely resemble insect sensilla in size, arrangement and shape (Callahan, 1977b, p. 117; Jewell et al., 1991, pgs. 87 & 94). The microlasers made at Bell Communications Research measure only one micron or less, are arranged in nice, neat linear arrays, and are elongated. As a matter of fact, virtually any shape can be laser etched, so there is no reason not to believe that insect sensilla can be replicated with stunning accuracy, if they have not already been by certain agencies. Transistors having dimensions smaller than a micron are routinely fabricated in numbers approaching tens of millions on a single conductor chip (Jewell et al., 1991).

The Office of Naval Research, for example, sponsors both man-made technology in this field (Grossman et al., 1991) as well as research on insect sensilla (Roshdy et al., 1972; Chu-Wang and Axtell, 1973) including research dealing with the insect's ability to detect electromagnetic radiation (Brown, 1963). Additionally, the U.S. Navy has utilized (in the Second World War) a large rectangular array of 42 dielectric rods for gunnery fire control purposes (reported in Kiely, 1953). Their support of studies investigating arthropod sensilla has expanded our knowledge of these candid structures.

On the other hand, the sensilla may collectively receive the EM frequency as mentioned above, but instead of directly causing a neuron to fire, they may alternatively induce a physiological change to occur directly beneath the cuticle. The EM frequency would then be detected by the insect as a physiological alteration, such as ion flow or hormone release, which would in turn be detected by the insect in a completely different part of the body. It is well known that some of the organic materials occurring in cuticle and insect blood (-OH, -CH, -NH groups and others) absorb strong between 2.4 and 4.0 µm (Evans, 1966b). Sense organs should then be relatively thin, as in olfactory chemoreceptors (Slifer, 1970) or transparent, such as occurs on *Melanophila acuminata*, where the apparent absence of the exocuticle may allow for efficient far-infrared detection (Evans, 1966b).

Because of the apparent difficulty in determining at what level we should test the insect (which is how "reductionist science" works), the first line of inquiry might best be made at the organismic or population level. Tautz (1978) obtained reliable behavioral responses only from intact animals, and rarely from isolated segments when studying caterpillars. Therefore, because both of these higher levels of investigation have proven instructive in the past, the tests to conduct, at this time, should be behavioral.

Scatter Surfaces

A discussion on electromagnetic energy would not be complete without the recent work on scatter phenomena. I have spent some time in the library reading books searching for scattering phenomena concerning EM waves on various surfaces. My search has shown that almost nothing is written from an entomological point of view, and little useful information could be pulled from the facts that I understood. However, it is a relevant topic, and most importantly, it has some bearing on this dissertation. Therefore, I will briefly introduce some of the major points and facts concerning scatter phenomena that I have picked up, and attempt to relate them to entomology as best I can.

Scattering theory and experimentation originated in the 1950's (Bennett and Mattson, 1989). Researchers investigated such things as the scattering of radar waves from the ocean surface. They measured the surface roughness of the Moon by analyzing the distortion of the radar pulse backscattered from the Moon to the Earth. Physicists studied the propagation of line-of-sight radio waves, some of which bounced off the Earth, as well as the scattering of sound waves by rough surfaces. A review appeared some ten years later entitled *The Scattering of Electromagnetic Waves from Rough Surfaces* (Beckmann and Spizzichino, 1963) which contains over 300 references.

The best example of light scattering in insects concerns the blue morpho butterflies. These butterflies do not possess the natural pigments in their wings so common among other butterflies. Instead, the blue morphs have what is known as a "structural color" rather than a "pigmented color". Visible light strikes the surface of a blue morph and becomes scattered such that the emitted light is dependent upon the angle viewed. Indeed, the wing color of the blue morpho changes from blue to various shades of blue and purples while adjusting the viewing angle. The predominant scattering color of blue is created from the diffraction/reflection patterns dependent upon the surface of the wing.

Although this example is well-known among entomologists, a lesser known scattering phenomenon was observed in 1965 involving the corneal nipple array, which is located on the surface of the compound eye of some insects. The corneal nipple array functions by decreasing reflection (scatter) in the visible region while producing a concomitant increase in the amplitude of the transmitted wave through the cornea

(Bernhard et al., 1965). The nipple array is actually an antenna array with a selective absorption of EM radiation in virtue of its size in relation to the incoming wavelength (size matching) and its impedance matching with the atmosphere.

A well known method utilizing scatter radiation for catching insects has been utilized by many an entomologist for capturing nocturnal insects, which consists of positioning a blacklight or a visible light, with a white sheet behind it as a backdrop. The insects attracted to this trap will be attracted to the scattered radiation emanating from the sheet and will largely ignore the actual light source. The type of scatter surface is extremely important to the catch as Pickens and his colleagues discovered in 1994. Their research found that a house fly trap involving a 40-W bulb and a reflector showed a significantly larger catch when an aluminum reflector was used than a white plastic reflector.

Utilizing his knowledge of scatter phenomena, Callahan (1957) was able to increase mating in the corn earworm above natural levels when he lined his mating cages with aluminum foil. Anecdotal information only adds to this because Kaae and Shorey (1973) once noticed that more moths and more mating pairs rested on illuminated leaves than on shaded leaves during the full moon. Quantaince and Brues (1905) mentioned that moths often congregated on stems of grass 20 to 50 ft. from an electric light, and Callahan (1957) noticed that the corn earworm adults do the same around a blacklight trap.

Molecular scattering takes on many different names depending upon the properties. The system is complex, but there exists Rayleigh center scatter (or Cabannes), Rayleigh wing Brillouin or Mandel' Shtam-Brillouin, Stokes and anti-Stokes Raman wavelengths. These scattering wavelengths are reported to be highly predictable for certain conditions such as coherent radiation. Under coherent conditions, for example, Stokes and anti-Stokes wavelengths will occur exactly the same distance away (measured in wavelengths) to the central coherent wavelength. What this means is that a coherent wavelength emitted from a molecule, say 490 nm, will scatter radiation such that a Stokes wavelength will be detected at 483 nm, and an anti-Stokes wavelength will be detected at 497 nm. These interference patterns are a characteristic of laser light (Jewell et al., 1991), and because they are so reliable, it may be that these scattering wavelengths, are used by insects to assist in identifying a particular molecule. If this were so, one might expect to find adjacent sensilla but of different sizes, set off by themselves, on the body of an insect. One sensillum would resonate to the peak wavelength, while the other would resonate to scatter frequencies, such as anti-Stokes. Their close proximity and likely interaction (quite possibly already shown by Markl and Tautz in 1975) would enable the insect to detect a particular coherent frequency absolutely.

The performance of an antenna, particularly with respect to its directive properties is considerably modified by the presence of the earth beneath it (Anonymous, 1974). This fact has been recognized for many decades at least, and many man-made antennal arrays are designed with this factor in mind. One of the factors to consider is the selective property of the ground. The effect of the ground can be to increase the intensity of the radiation at some vertical angles and to decrease it at others. This means through no inherent characteristic of the antenna itself, the antenna proper can be selectively tuned to certain polarized frequencies by virtue of its interaction with the surrounding ground. One effect of the ground is to simply reflect the incoming wave. This type of scatter is the simplest.

If indeed a wave is reflected, then these reflected waves may interact with the direct wave in various ways. This interaction will depend upon the orientation of the antenna with respect to the ground, the height of the antenna, its length, and/or the characteristics of the ground. Polarized waves can be unchanged or phase shifted 180° on reflection. Interaction of the incoming and reflected waves modifies the manner in which the antenna receives it. Predicting the type and degree of interaction, however, is mathematically very difficult. There is no question, however, that the interaction exists, therefore, it needs to be taken into account in a discussion such as this.

The prevention of scattered waves from the ground, reflected or otherwise can be achieved by conducting the received waves away from the antenna and was described in The ARRL Antenna Book (1974) as such:

> The ideal grounding system for a vertical grounded antenna would consist of about 120 wires, each at least ½ wavelength long, extending radially from the base of the antenna and spaced equally around a circle. Such a system is the practical equivalent of perfectly conducting ground and has negligible resistance. (p. 61)

This system, or anything resembling it, has not been seen by this student on any insect. Therefore, I will make the assumption that some scattering off the insects's cuticle is occurring, and so being, also must be considered into the discussion of EM frequencies, insects, and antennae.

The number of different surface terrains found on insect cuticle cannot be covered in this response, even if they were all known. It is often noted however, that sculpturing of the integument is often species specific (Pilgrim, 1991a). Instead, I can only point to a few examples drawing from my own limited experience.

Since reflection is the simplest scattering concept to understand, I will spend some time discussing this. If one reexamines the quote just given, the number ½ or 0.5 seems to jump out as being critical. If the area around the vertical antenna can be completely conductive should a radial system be designed of at least half a wavelength, then observing a similar radial phenomena in nature with similar dimensions would be good circumstantial evidence for a scattering surface and that the insect used its sensilla as an electromagnetic antenna.

It may also be that electromagnetic waves may scatter off the insect sensilla themselves. Just recently, Sajeev John (1991) described strongly scattering dielectric microstructures. Certain dielectric microstructures have no propagating modes in any direction for a range of frequencies and exhibit what has been termed a "complete photonic band gap" (John, 1991). Therefore, if insect sensilla are operating as dielectric waveguides, then the presence of numerous adjacent sensilla could severely affect scattering, which in turn affects how the antennae receives the wavelengths. This can occur in three ways- constructive interference, destructive interference, and resonance.

Helical and corrugated sensilla are found on many insects. These sensilla types may support the propagation of slow surface waves and thus find important application in delay electronic devices (Callahan, 1975a). It may be that waveguides with helical striations can discriminate between polarized EM radiation. Already, we know that one of the four basic characteristics of an antenna is its polarization (G.R.I.P.), therefore an antenna can distinguish between two seemingly identical wavelengths but with different polarizations. The helical striations of the waveguide would simply guide the wave in one direction but inhibit radiation flow in the opposite direction. This would come about due to the properties of the antennae acting as a surface waveguide where propagation of the wave occurs on the outside of the antenna. What this means is that some insect sensilla might be able to discriminate between enantiomers, since enantiomers differ only in their ability to bend polarized light (Armstrong, 1989). Davis (1988) has shown that a sensillum on a mosquito cannot discriminate between enantiomers, however, Kafka and colleagues (1973) showed sensilla on both a grasshopper and the honeybee could discriminate between enantiomers. How some sensilla discriminate between enantiomers while others do not, should be explained by antennal morphology since all characteristics of a particular antenna are irreversibly linked to its structural make-up.

Electromagnetics: an Overview

Electromagnetic waves were theoretically described for the first time by J.C. Maxwell in 1864 and established experimentally in 1887 by H. Hertz. Electromagnetic radiation is composed of two phenomena. The first is an electric field, and the other is a magnetic field. These two phenomena orient perpendicular to one another while interacting, and together form an electromagnetic field. Oersted first discovered the effects of an electric current on a magnetic needle in 1820, and therefore, showed (without understanding) the strong interdependence each field had for the other. Their interdependence means they are not normally separated in nature, such that detection of an electrical field usually denotes the presence of a magnetic field. Along the same line, a change in either the electric or magnetic field will result in a change in the other. Even though they are inextricably related, one important difference to keep in mind is that electricity is an energy, while magnetism is a force, which means that a magnetic field is able to do work. The biophysical properties of electrical currents and magnetic fields differ, and these properties have important implications for sensory perception.

Electromagnetic radiation travels in sinusoidal waves through free space at the speed of 300,000 km/sec, which was first established experimentally by A.H. Fizeau in 1849. They slow down when passing through a medium and refract, or bend, at all interfaces where there is a change in density. If the angle with which they strike a new interface is severe enough, reflection is said to take place. Varying degrees of reflection and refraction may occur depending upon properties of the new medium and the wave's angle of incidence.

Electromagnetic energy does not all behave the same nor is it perceived the same way by a given organism. This is due to the wavelength of the electromagnetic (EM) wave as well as the energy it contains. For example, visible radiation can have very small changes in wavelength, but our eyes perceive these subtle changes as completely different colors (i.e. yellow and green). The radiations that have wavelengths longer than visible light include infrared, microwave, and radio.. The radiations that have wavelengths shorter than visible light include ultraviolet, x-rays, and gamma rays.

The wavelengths in the visible range include what we call 'colors'. By definition, these wavelengths make up collectively one 'octave'. All other EM radiation is invisible to the human eye but, of course, can be detected by other means. Infrared radiation is what most people refer to as heat. However, thermal, or convective heat can be produced by almost any form of EM radiation, such as light rays, x-rays, and even high intensity radar beams (Callahan, 1965a). Intermediate- and far-infrared energy along with near-infrared together constitute 17 octaves, which means they span a range 17 times larger than the visible wavelengths. Additionally, microwaves make-up 8 octaves. Scientific papers dealing with the visible range and their effects on insects all far exceed the number of papers associating the infrared or microwave wavelengths. Because these 25 octaves have been relatively untapped by entomologists, there are countless potential discoveries to be made.

Table 2-1. Infrared spectrum designated by wavelength range.

Infrared (familiar name)	Wavelength range
Near-IR	0.8-2 µm
Intermediate-IR	2-15 µm
Far-IR	15-1000 µm

Generally speaking, the longer wavelengths are considered low energy and the shorter wavelengths, high energy. This has led many researchers to believe that organisms do not detect very long wavelengths because their energy is too low, or that very short wavelengths are destructive to life because of their high energy, such as cosmic rays producing chromosomal breakage in *Drosophila melanogaster* (Reddi and Rao, 1964). Smith and colleagues (1963) have shown a remarkable sensitivity among insects to low-intensity radiation, which suggests that insects may have developed systems to detect low intensity levels with which we are still unfamiliar. Although it is understood that the most important wavelengths for organisms are in the visible, infrared and ultraviolet regions, and that these wavelengths are short enough to be received selectively and to penetrate the skin with moderate absorption, growing evidence does show that apparently *all* forms of radiation are biologically active in some degree, even gamma radiation (Brown, 1963) and x-rays (Smith et.al., 1963). The detection of these apparently destructive wavelengths *in vivo* may in part be due to the fact that biological systems have defensive systems for protection against the adverse effects of electromagnetic fields (Presman, 1970). It follows that with adequate protection, an insect may be able to use these particular wavelengths to their benefit.

Biological investigations have shown that organisms of the most diverse kinds- from unicellular organisms to man- are sensitive to a constant magnetic field and to EM fields of different frequencies (for reviews see Barnothy (1969), Presman (1970) and Popp et al. (1989)). The effects of multiple exposures on the organism are sometimes cumulative. Exposure to strong fields usually leads to adaptation to subsequent exposures, whereas exposure to weak fields leads to progressively greater changes in the organism (Presman, 1970). Surprisingly, some of these investigations have found an effective energy tens of orders less than the theoretically estimated effective level. A very important feature of these biological effects is that they are often produced by fields of extremely low intensities. This naturally suggests that organisms have systems which are especially sensitive to EM fields and as yet have no analogs in man.

In most cases, EM fields cause disturbances in the regulation of physiological processes during embryonic development and during growth, which is the period when the defense mechanisms do not exist or are not fully developed. Unfortunately, most of the physiological mechanisms that lie behind biocommunication by means of electromagnetic fields still remain unexplained (Breithaupt, 1989).

Interactions between organisms and EM fields take one of three general forms. To some extent, they are all forms of communication and include:

1. The effect of EM processes taking place in the environment on the functioning of living organisms.
2. The role of EM processes taking place within an organism in the vital activity of organisms.
3. EM interconnections between organisms.

By means of EM fields and depending upon the frequency, information can be transmitted through any medium inhabited by living organisms and in any meteorological conditions- during the polar day or night, in river and sea water, within the earth's crust and finally, in the tissues or organisms themselves. Additionally, reports indicate that entire organisms are most sensitive to EM fields, whereas isolated organs and cells are less sensitive, and solutions of macromolecules even less so (Presman, 1970). Tautz

(1978) came to the same conclusion when studying the vibration receptor hairs on the caterpillar, *Barathra brassicae*, when he found that recordings from hairs needed to be made from intact animals because it was not possible to get reliable responses over sufficient duration from isolated segments.

For this reason, when studying the effects of EM fields on organisms, 'reductionist science', such as electrophysiological experimentation, may not be as effective a scientific methodology in reaching the correct conclusions as will sound behavioral experimentation on whole organisms or even populations of organisms. Investigation of these functions must proceed from complex biological systems and processes to progressively more simple systems and processes. This gradual descent down the hierarchy of systems should help to avoid the confusion that is so often generated by conflicting results conducted upon separate parameters of the same system.

All EM fields are based upon waves. Most of these waves may take the classic form of a sinusoidal wave, however, other waves or oscillations may impinge upon these waves thus forming a *modulated* wave. The sinusoidal waves vary only with sine and cosine laws, but modulated waves vary with the perturbing wave as well as the carrier wave. Obviously, these modulated waves are more complex but always include additional information that may be necessary for communication. It is important for living systems to have highly coherent carrier oscillations for purposes of bio-communication, but the effects may well be generated by modulation of the carrier wave.

For example, Smith (1989) reported that human patients who complain of allergic responses to microwave cookers often show on testing no reaction at the microwave frequency when it is highly coherent. However, they react strongly when the frequency is modulated with extremely low frequencies commonly generated while the turntable in the microwave cooker rotates. Furthermore, radio communications transmitted or received by helicopters are often modulated by the spinning rotors (Warnke, 1989b).

For insects, waves may be modulated by the 60 (Hertz) Hz “flicker frequency” alternating electric field in the United States (50 Hz in other countries). The exoskeleton of insect antennae is highly reflective of visible radiation (Callahan, 1990). This means an insect within the vicinity of an alternating current will be flickering, by virtue of reflection, at that frequency. If the insect is indoors under artificial lighting, then this flickering of visible wavelengths off the insect’s body could very well be modulating any incoming wavelength.

Animal Perception

That organisms respond to varied forms of EM radiation should not come as a surprise to any scientist who is aware that electromagnetic radiation must have existed before life began (both Genesis, 1:3 and Keeton and Gould, 1986) and that all life absolutely must have developed under its influence. The influence of the chemical environment has often been pointed out, while another part, the electromagnetic environment, has too often been neglected (Kroy, 1989). Living systems are subject to the laws of physics and particularly the physics of electromagnetic fields, just as much as they are subject to chemistry. However, not all life will respond in the same way to these fields and one challenge is to determine how a particular organism responds to various forms of EM radiation.

The short-term effects of EM fields on the behavior of animals is revealed in changes in general motor activity, attempts of the animal to escape from the acting factor, and orientational reactions to EM fields. Smith (1989) reported that human subjects could develop allergic reactions when exposed to particular EM fields. In general, Smith continued, there are many biomedical systems which have reported sensitivities to low level electromagnetic fields. Laboratory experiments with *Euglena* show that when exposed to a frequency of 5-7 Megahertz (MHZ) they orient, in motion, parallel to the electric lines of force (reported in Presman, 1970). Additionally, specific motor reactions of paramecia to EM stimuli of various kinds have been reported (Presman, 1963a,b).

Long-term effects of EM fields on the behavior of animals are often revealed in one or more delayed responses usually measurable as physiological changes or as delayed behavioral responses. Keplinger (1958) exposed the back of a rat to intense 1.25 cm waves, which are completely absorbed by the skin. This led to high-frequency oscillations of the biopotentials commencing fully seven minutes after irradiation. The slow response often shown in response to various stimuli is eloquently described by Aladzhalova in 1962 with regard to brain activity.

> One of the characteristics of the slow control system is the fact that it does not react to an insignificant single (chance) external disturbance. Its reaction to an environmental factor acting more or less systematically takes several hours and can be directed not only towards overcoming the produced changes in the internal environment, but also towards active alteration of the level of activity with due regard to the possible effect of the new factor. (quoted from Presman, 1970)

In many cases EM fields cause disturbances in the regulation of physiological processes, mostly during embryonic development and during growth (the period when the defense mechanisms do not exist or are not fully developed). An examination of the nature of these disturbances indicates they are due to the effect of the EM field on the EM processes specifically involved in the regulation of physiological functions (Presman, 1970).

An interesting theory also maintains that natural and artificial fields affect biochemical processes in organisms by affecting the water in which these processes take place. Water is involved in almost all biochemical processes, either directly or indirectly. Therefore, if water could store energy, it could influence the biochemical processes that involve it. This hypothesis finds support from researchers who have determined that coherent EM fields can be stored in H_2O for more than a month after exposure (Choy et al., 1987).

Some animals do possess sensory organs apparently designed for the detection of EM fields or waves. Well known examples include electrosensitivity in many fish such as the hammerhead shark as well as the bill of the platypus, the detection of ultraviolet radiation by the bee, and infrared prey detection by snakes and owls. Humans do not possess these capabilities, so understanding these abilities is more difficult for us to comprehend then, let us say, vision, which is surprisingly similar across many animals. Certain exceptions do turn up occasionally, such as the eye of slugs, which has been shown to respond to IR radiation (Newell and Newell, 1968).

Sensory perception may be involved with physiological changes or morphological changes in organs and tissues of animals produced by a single exposure to EM fields of high intensity or cumulative effects from repeated exposures produced by low-intensity EM fields (Presman, 1970). Indeed, there may be specialized sense organs that perceive these stimuli, such as the ampullae of Lorenzini on a shark's snout (Kalmijn, 1977), which are sensitive to weak electrical stimuli produced by muscle contractions of bony fish and are, of course, important to the shark for detecting its prey. These organs can respond to fields as small as one microvolt per meter (Kalmijn, 1977; Murray 1965) which is several orders below typical action potentials (Jungerman and Rosenblum, 1980).

Electromagnetic "auras" called electroauroagrams were detected 25 cm from an isolated frog nerve (1 mV), isolated frog muscle and heart at a distance of 14 cm, and human heart and muscle at a distance of 10 cm (Gulyaev, 1967; Gulyaev et al., 1967). Detection of these fields is likely for many animals, because many terrestrial animals, including various species of insects, birds, and furred animals, produce electrical fields of relatively high amplitudes (Warnke, 1973; 1975). The wings of flying insects and birds together with their surroundings are working as electric field generators, which build up relatively strong Coulomb forces at the outside surface (Warnke, 1989a). Electrical field intensities from animals in wind channels were reduced to nearly zero when metal wind channels were used. Wind channels made from wood were more similar to electric fields determined in the open air (Warnke, 1989a).

Detection of Electromagnetic Fields by Insects

Insects are a strange crew, but this is what makes them so interesting to me. They exhibit various behaviors that cannot be explained by conventional theories, but are consistent with the hypothesis that insects detect electromagnetic radiation. One of these apparent anomalies concerns the ant, *Trachymyrmex septentrionalis*, which always builds mounds with a slope in one predominant direction. Tschinkel and Bhatkar (1974) reported that destroying the mound prompted the workers to build a mound facing the same direction to within 3.2°. Some common environmental factor to which this species oriented seemed improbable because each ant colony chose an orientation independent of adjacent colonies, and yet each one would rebuild their same mound in the same direction after it was artificially destroyed. On the other hand, mound orientation just might be explained by an environmental factor influencing the individual colony, since bringing the colony indoors causes them to make a completely circular mound. How all the workers come to agree on building a mound with the identical orientation is yet another question waiting for an explanation. Could electromagnetic waves be directly affecting this behavior either in the environment or via intraspecific communication? Examples will follow of how social insects may be utilizing EM fields for communication purposes.

It is possible for high electrical field intensities to occur at the tips of antennae. This can be visually depicted as an intensive bunching of the field lines, or peak current conduction. The same basic process occurs at the microtips of an insect's body (Warnke, 1989a). Charged particles selectively adhere to insect sensilla when the cuticle itself is charged (Warnke, 1989a). This knowledge had been used for years by NASA wherein electrets were used to collect charged particles and vapors from the air in pollution studies (Pillai et al., 1974). No attraction of charged particles occurs toward insect sensilla when no electrical charge has been applied to the underlying cuticle. Indeed, many researchers have independently determined that the concentration of molecules can be several orders of magnitude higher on the cuticle layer, after just one second, than in the airstream by which they were introduced (Adam and Delbrück, 1968; Steinbrecht and Kaissling, 1974; Mankin et al., 1977; Kasang, 1978).

Contact chemoreceptors or gustatory chemoreceptors have a terminal pore at the tip. It was discovered by Callahan (1975a) that charged particles are attracted to the electret properties of the sensilla and move along the trichodea to this single pore where they collect in clumps.

Light produced at the tips of structures comes from gas molecules that have been excited to release energetic electrons during collisions with an avalanche of electrons. The avalanche is caused by the strong electric field that propels electrons from the pointed exposed surface where forces binding ions to the surface are weakest (Golde, 1973). This action results from the "point effect" which states that electrical field intensity will be highest at the tips (i.e. St. Elmo's fire).

Biological matter lighted by strong electrical fields is not uncommon in nature. Schonland (1950) measured point discharge from plants. He found that during thunderstorms the flow of electricity to earth was considerably greater than the flow from earth during fair weather. If a thunderhead is particularly heavily charged he noted that even leaves and blades of grass may glow at the tips because of intense ionization activity.

Callahan and Mankin (1978) subjected five insects to a large electric field and they all emitted visible glows of various colors as well as ultraviolet. The insects displayed bluish white light from various external points on their bodies such as the distal tip of mandibles, ovipositors, antennae, leg joints, and red, green, or orange flares at or near the spiracles. Any species of insect can be made to emit visible radiation if it is placed in an alternating electric field between 2 to 3 kV/cm (Callahan, 1980). The areas that light up are also the areas that contain the sensory organs.

Insect sensilla can be stimulated mechanically in regions adjoining highly resistant structures (sclerites) because of increased field intensities. This suggests that the assimilation of electric fields is ultimately reduced to the detection of mechanical energy (Warnke, 1989a).

Detection of electromagnetic energy can be accomplished by insects in several ways. Bees regularly pull their antennae through a cleaning gap (antenna cleaner) at the frontal extremities, thus positively charging them (Warnke, 1989a). In fact, virtually all insects are known to do the same thing. Any dielectric having a conductivity greater than that of air will decay to zero after a short time (Mankin, 1976). For this reason, insects should be continually charging themselves, which they do, maybe in an effort to compensate for this problem.

Simply stated, a charged antenna will be able to detect charged particles. Electromagnetic fields around insects created by the atmosphere should be more pronounced in flying insects, due to the grounding effect when in contact with the earth's surface. This means insects should be more sensitive to certain EM fields during flight, and many insects do search for scents while on the wing.

Entomologists are aware that insects seek shelter during rainstorms which traditionally was explained as an escape response to the highly dangerous rain drops plummeting from the sky. Man-made dielectric antennae do not work efficiently when dew or excessive moisture collects on them (Kiely, 1953), so reason dictates that if insects use their sensilla as dielectric antennae, avoiding excessive moisture would be in their best interest. Additionally, the electromagnetic field strength accumulating at tips, as described above, is predominantly a function of the relative atmospheric humidity (Warnke, 1989a).

Bees are particularly aggressive when subjected to high atmospheric activity in the 10-20 kHz range (Warnke, 1973). If this action came about through changes in electric charges about the bee, then one would expect action on the part of the bee in response to this change. Groups of bees kept in earthed metal cages with a relatively high atmospheric humidity will lose their charges. The immediate fluttering of the wings which commences may occur in an effort by the bees to recharge themselves through friction with the air. Indeed, as soon as atmospheric ions are added to a Faraday cage, fluttering ceases abruptly (Warnke, 1989a). Frictional or tribolelectric effects contribute strongly to an object's charge density. A beeswax disk freshly washed in distilled water exhibited a surface charge density of 12×10^{-11} cl/cm^2, however, scraping it only once across a paper towel increased the charge density to 1.9×10^{-9} cl/cm^2 (Mankin, 1976).

Beating wings of flying insects produce extremely low frequency (ELF) radio emissions and are detectable with a tuned radio frequency radio receiver (Koemel and Callahan, 1994). Different ELF frequencies can be produced by the two wings and one noctuid moth produced seven nonharmonic radio frequencies simultaneously. In fact, more than 5000 samples of flying insects, tested one at a time, produced radio frequencies (Koemel and Callahan, 1994). Electromagnetic fields created during the flight of the bumblebee and mosquito were also detected by Gulyaev and his co-workers over twenty years ago (Gulyaev, 1967; Gulyaev et al., 1967).

At the other end of the electromagnetic spectrum, Hudseph (1970) found the maximum radiant energy across the moth blackbody[5] to be highest between 7 and 14 µm. These infrared wavelengths are only the maximum values in a wide range because every object at a temperature above absolute zero emits infrared radiation (Barnes, 1963). Callahan and Lee (1974) found the corn earworm moth to emit a 10 µm infrared signal which is chopped (modulated) by the wings. When all insects fly, they raise their background temperature to a considerable degree above the background temperature of the atmosphere (Callahan, 1968). Earlier research by Duane and Tyler (1950) compared the total emission spectrophotometric curve of the cecropia moth with that of a blackbody at the same temperature, and reasoned that the male could detect a female in the 3 to 11 µm region against a cool night background. Fifteen years later Callahan (1965c) reported that the corn earworm moth could detect an infrared emitter in the 8-13 μm range in a totally dark room. Callahan (1965c) calculated that the moth thorax, *Herse cingulata*, would be easily detectable to a receiver up to 1 km away when taking into account the body temperature and wattage produced. The fact that these moths, and no doubt others, emit infrared in the same range that they are designed to detect, points to the likelihood that moths use this system as a navigational aid. Indeed, Hackforth simply stated in 1960 that 'any object at a different temperature than the surroundings can be detected'. It is reasonable to assume that moths, and other insects, have taken advantage of this fact.

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[5] A blackbody is any object that absorbs or receives all infrared radiation. Objects that absorb in lesser degrees are termed 'gray bodies'. Blackening a surface will help to approach the ideal blackbody (approaches unity). A mirror radiates and absorbs infrared wavelengths poorly and therefore has an emissivity close to zero.

Body lice were found to be more attracted to the blackbody side of an experimental set-up over an aluminum (reflective) side, even though both were maintained at the same temperature (Broce, 1971). Additionally, this orientation toward a blackbody infrared (IR) source was accomplished in the absence of convective heat. Broce explained this response as a necessity for the newly hatched larvae to find a host. The lice detected this blackbody source at a distance of 3.25 cm, but were unable to do so at 4.75 cm. This threshold distance agreed with the threshold distance for bedbugs as reported by Rivnay (1932). Hence, the reaction to blackbody IR is advantageous, because by actively moving only when the host is in close proximity, the chances of being rewarded by a blood meal are increased.

The wavelength of peak intensity for a warm-blooded animal is ca. 9.5 μm (Bruce, 1971). Therefore, the emissivity in the infrared for homing in on a moth might not be too different for homing in on a human. Human skin is an almost perfect emitter of infrared radiation in the spectral region beyond 3 microns (Barnes, 1963). Emissivity is a direct function of absorption, and since absorption in turn is a function of wavelength, it follows that any given object may be transparent for one part of the spectrum and totally absorbing or "black" for other wavelengths. For example, human skin is relatively transparent to visible light and to infrared radiation of wavelengths shorter than about 2 µm. Therefore, skin pigmentation produces great differences in the absorptive and reflective power of skin for these parts of the spectrum. However, this pigmentation plays no role in the longer wavelength region (Barnes, 1963). All humans, regardless of race, were indistinguishable when viewed under infrared devices (Barnes, 1963). Research in the infrared had led to earlier developments like the Sniperscope, the heat-seeking head of the Sidewinder missile; the horizon sensors used in the stabilization of spacecraft, the temperature-measuring radiometers of the Tiros weather satellites, and the Venus probe, Mariner II. A wide assortment of sensitive infrared instruments are available for passive detection, temperature measurement, communication, viewing, and thermal photography, (Barnes, 1963).

Response of Insects to Electromagnetic Fields

Much of the research conducted with insects and EM radiation focused on killing or injuring the bugs (Nelson, 1967; Frings, 1952), and not upon any communication system. Tilton and Schroeder (1963) killed immature insects in kernels of rough rice by treating with a gas-fired infrared heater. Nelson and Kantack (1966) used a 39 megacycle radio frequency which killed all stages of the Indian-meal moth in a matter of seconds.

Microwaves (12.25 cm) were used to kill the granary weevil and the flour beetle as reported by Baker and his colleagues in 1956. Radio frequencies were again chosen to kill the wax moth (Nelson, 1967) and rice weevil (Nelson and Stetson, 1974), where death was generally thought to come about through differential heating of the insects vs. the foodstuff (Nelson and Rhine, 1966). For example, Nelson (1967) calculated the heating rate for rice weevils to be 1.8 times the heating rate for the wheat. The distinguishing feature between these "killing" frequencies and communication frequencies lies in the energy of the wave. These wavelengths can theoretically be used by insects for communication. However, their energy must be reduced substantially.

W.H. Whitcomb, his student, J.C. Nickerson, and Callahan collaborated on a short research project involving a worker ant, *Conomyrma insana* (Buckley), and infrared emissions (Callahan et al., 1982). They found that the worker ant was attracted to the *far-infrared* emissions from wax and petroleum candles (remember, heat is generally associated with near-infrared). The results were determined by utilizing selective filters designed to block out certain wavelengths. Radiation emanating from the candle in the visible range was not attractive to the ant. However, if filters allowing far-infrared to transmit were used, the worker ant made a "bee-line" directly towards the source and after reaching a point ca. 5 cm (or less) from the base, kept circling the candle similarly to a moth circling a lightbulb or candle flame. It is likely that far-IR detection can be accomplished by sensilla of appropriate size, however, there is also the possibility that insects may "see" IR radiation via the ommatidia (Callahan, 1965b) or ocelli (Callahan, 1969).

Various species of moth and larvae were subjected to infrared radiation with wavelengths in the 1-30 µm band (Callahan, 1966). High intensity infrared focused into the eye killed moths in an average of 60 sec. at 120°F. Low intensity infrared focused on the antenna or eye elicited flight, antennal responses, or sexual responses, at 85 to 92°F. Low intensity infrared at 92°F focused on the ocelli of larvae elicited fecal pellet deposition, searching, and head scanning. Fifth instar corn earworm larvae were subjected to the radiation for 15 to 40 sec., before becoming active, which consisted of depositing a fecal pellet, chewing with their mandibles, and moving toward the IR source while scanning it with the head. Noctuid adults responded by vibrating their antennae immediately. The coiled proboscis immediately went into a frenzy of movement. Curiously, sphingid moths and saturniid moths were much slower to respond with antennal movements. The four species of night-flying arctiid moths were by far the most sensitive. They all responded by curving the abdomen and feeling toward the source with both legs and antenna, and attempted to touch with their abdomen objects brought within their range. One second of high-intensity radiation of 1 to 30 µm elicited flight and sexual responses from these four species for a period of 10 to 20 minutes. Five to ten seconds of low intensity IR induced similar responses.

Work in England with the rusty tussock moth, *Orgyia antiqua*, gave indirect evidence that this species is attracted to the opposite sex by high frequency radiation and individuals of this species were found to orient upwind in response to the presence of the opposite sex (Laithwaite, 1960). Fabre (1912) also reported orientation between insects upwind of one another. Laithwaite further speculated that the pectinate antenna of the male serves as a diffraction grid for reception, presumably of the female, and was one of the first researchers to suggest that insect antennae might be capable of detecting electromagnetic energy.

Four years later Evans (1964) showed that a buprestid beetle, *Melanophila acuminata*, possessed a distinct infrared sense organ located not on the antenna, but on the mesothorax adjacent to the coxal cavities. Although several reports had found that insects, such as mosquitoes (Burgess, 1959), respond to infrared, this was the first reported insect infrared *organ*. The radiation used to elicit a response was incoherent infrared radiation between 0.8 and 6.0 μm, with a maximum sensitivity between 2.5 and 4 μm (Evans, 1966a). Evans felt that these sense organs responded to IR radiation produced from forest fires many kilometers away, possibly 100 kilometers or more (Evans, 1964, 1966a). Responses measured included a form of antennal twitching on the side of the body being stimulated, and this only occurred when the sensory organ was stimulated, not the antenna. In fact, stimulation of no other part of the body could elicit this reaction. The twitching response occurred only after exposure to the radiation for as little as 33 msec, which points toward a legitimate radiation detector and not a response by means of some secondary reaction to convective heat. This discovery does not, however, preclude the beetle's sensitivity to heat as well. When light from microscope light is filtered to allow only wavelengths greater than 1 μm (near infrared) to pass, beetles will aggregate on the side of the cage where this stimulus is presented (Evans, 1966a). Additionally, beetles aggregate toward a heated element in the cage. Beetles lose this ability after antennectomy (removal of the antennae). This suggests that near-infrared incoherent receptors may be located on the antenna, while far-infrared to intermediate-IR coherent receptors may be located within the specialized infrared sense organ (Evans, 1966b).

Adult females of the spiny rat mite, *Laelaps echidnina*, also respond to incoherent infrared radiation in the narrow band between 4.4 and 4.6 µm (Bruce, 1971). Much like *Melanophila*, the behavioral response consisted of rapid vertical movements or a single laterally directed movement of the forelegs. The spiny rat mite is able to discriminate among several IR wavelengths and is able to accomplish this at relatively low intensities. These mites have no optical system, and they live in virtual darkness. The predominant sensory structures on the body are numerous setae. On tarsus I of the foreleg, tapered setae are the only observed sensory structures.

Infrared detection had already been shown with other insects, such as the mosquito, but the response, probing behavior, was reported to be elicited in response to thermal or convective heat as well as to moisture (Burgess, 1959).

Incoherent radiation sources were incapable of eliciting reactions in moths (Eldumiati and Levengood, 1971; 1972) as well as coherent radiation from Klystrons (0.8 to 3.5 cm), a Gallium Arsenide diode (0.85 µm) or a pulsed near-infrared laser. Positive results were obtained by Callahan (1968, 1969) who first used coherent radiation from lasers in insect behavioral experiments. Tests using a cyanide laser at the Georgian Institute of Technology[6] demonstrated that the corn earworm moth, *Heliothis zea*

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[6] USDA Coop. Agreement (1966) 12-14-100-9071 (33); Final Report Project No. A-985, Dec. 1970, Georgia Institute of Technology.

(=*Helicoverpa zea*) did respond by attraction to 337 µm radiation. This finding was supported by Eldumiati and Levengood (1971) who additionally found that the corn earworm and the fall armyworm, *Spodoptera frugiperda*, were strongly attracted to radiation of 311 µm wavelengths. Additional experiments indicated that the 337 µm wavelength induced changes in the activity of the moths and reduced mating potential (Eldumiati and Levengood, 1971). Under different conditions, Turner and colleagues tested corn earworm, fall armyworm, and cabbage looper adults (*Trichoplusia ni*) but found no attraction toward 28, 118, or 337 µm radiation produced by a laser (Turner et al., 1977).

Just a few years later the Glagolewa-Arkadiewa "mass radiator" was used to further test the response of insects to pure electromagnetic radiation. The mass radiator was used to transmit far-IR radiation upon several insects in order to record their behavioral responses, if any (Callahan, 1971). The responses were amazing. All insects tested responded to the mass radiator with antennal movement. Three mated corn earworm females were stimulated to oviposit within a few seconds of exposure to the radiation. Wasps immediately exhibited the antennal cleaning response, and fire ants responded by violent movement of the legs and antennae. Not a single response from any of the insects tested occurred when the antennae were cut off. One year later, Eldumiati and Levengood (1972) found extremely strong attractive responses of insects to far-IR radiation as well.

Electrophysiological responses were obtained from a saturniid moth when the antenna was exposed to incoherent as well as coherent light of 6328 Å (633 nm) low intensity laser radiation (Callahan, 1968). The fact that antennae respond to visible frequencies was just as important a discovery as the response to coherent radiation. Behavioral responses to broadband IR in the 1-15 μm range (far-IR) have been reported from *H. zea* (Callahan, 1965b), *Aedes aegypti* (Mangum and Callahan, 1968) and a braconid wasp, *Coeloides brunneri* (Richerson and Borden, 1972). Responses to narrowband radiation in the range 2-6 μm have been reported for *Melanophila acuminata* (Evans, 1964) and for an acarine, *Laelaps echidnina* (Bruce, 1971).

Electrical fields

The red imported fire ant, *Solenopsis invicta,* is attracted to electric fields (Gnatzy and Tautz, 1977). Attraction is directly proportional to field strength for both DC and AC current. Ants began to leave the source within seconds of the electrical source being disconnected, but the response was longer for the AC current which suggests that they may be able to differentiate somehow between AC and DC current. Other than this, no other behavioral differences could be distinguished from their responses to either DC or AC current.

When the electrical disks were covered with a plastic wrap, the ants no longer responded. These results suggest that the ants may have to come into contact with the conducting material to respond (Gnatzy and Tautz, 1977). The plastic wrap need only be 13 μm thick to prevent any response. Since an electromagnetic field can easily penetrate plastic wrap, the possibility exists that exposed conducting material may be necessary for detection. It also may be that a thin molecular layer may exist on the disks which in turn may be "pumped" by the electrical field (see section on molecular emissions). The observed responses could not have been a "natural" attraction since the ants responded to voltages of less than 10 V, but they responded proportionally up to 110 V (energy far above that found in nature) even though the ants could electrocute themselves quite nicely at 60 V.

Interesting orientation reactions have been observed in ants whereby a super high frequency (SHF) field (10,000 MHZ) caused the insects to orient their antennae along the electric lines of force (Jaski, 1960). Additionally, the ants lost the ability to "communicate" the location of food to other ants (Jaski, 1960). It is of interest that the length of the antennae of the large ants used in these experiments was almost a quarter of the wavelength. A relation between wavelength received and length of the ants' antenna, suggests the antennae proper are operating as electromagnetic antennae. Insect antennae are hollow and are covered with wax, which further means that the antennae may be operating as tubular dielectric waveguides. Other experiments with ants indicate the possible existence of intercommunication based on ionizing radiation (Khalifman, 1965; Marikovskii, 1965).

The effect of electrical fields upon social insects may be more profound than the effects upon solitary insects since communication is so vital to the existence of insect sociality. This communication process, which is at the moment not well understood, may be mediated by electromagnetic phenomena. Not only ants, as I have mentioned in the paragraph above, but bees when subjected to an alternating electric field are also no longer able to recognize one another (Warnke, 1989a). Additionally, the highly social activity of gallery building in termites is influenced by electric fields. When the termites were shielded by various metals, earthed or unearthed, gallery-building was suppressed for about 8 to 14 days, compared with unshielded groups (Becker, 1976a).

An electrical field gradient of 10 to 62.5 V/cm immediately reduced the activity of *Drosophila* but had no effect on the blowfly, *Calliphora* (Edwards, 1960a). During the period of reduced activity, those insects who were not walking about were usually observed vigorously rubbing together their front legs and cleaning their wings. Both E.C. Okress (reported in Callahan, 1967) and Warnke (1989a) hypothesized that insects do this in order to recharge certain cuticular regions of their body. Edwards suggested that the response of these insects was based upon the detection of the accumulation of charges, possibly static charges, on their body (although no mechanism as to how the insects accomplish this was given) and that larger insects may distribute the charges more effectively, therefore explaining why the larger fly, *Calliphora*, was not affected while the smaller fly, *Drosophila*, was.

Picton (1966) showed that *Drosophila* respond to weak magnetic and electrostatic fields, and Levengood (1962) found that an electric field affected *Drosophila* growth which he attributed to variations in air-ion densities. Schneider (1975) showed orientation in the beetle, *Melolontha vulgaris*, is strongly affected by electric charges, and Maw (1961) discovered that the rate of egg-laying increased when the insects were screened from fluctuating (modulating) natural EM fields in the presence or absence of an artificial electrostatic field of 1.2 V/cm (close to earth's electric field.) The same effect was observed when the natural fields were excluded, and replaced by artificial fields (0.8 V/cm) that fluctuated like natural fields.

Anecdotal information about Diptera (flies) increasing their activity before a storm are thought to be related to these electrical charges. Although Edwards (1960) could not support the claim that this behavior was dependent upon potential gradients found in nature, he was able to increase flight activity of *Calliphora vicina* by increasing positive-ion densities above that which would be found in nature. Peak activity was found to occur about 45 minutes after first exposure, however, the flies acclimated about 15 minutes after the peak and remained so. No effect was observed with negative ions. Becker (1963b) found that electrostatic fields 100 x greater than the earth's electric field rendered flies inactive.

Electric fields might also act as a stress stimulus. Bee swarms became very restless when exposed to an electric field of 11 kV/m, and the swarm temperature rose sharply (Warnke, 1976a,b).

> Defense of social territory was intensified to such an extent that members of the same swarm attacked one another. After a few days of the field influence the bees tore their brood out of their cells, and no more fresh broods were established. Similarly, honey and pollen were used up and no more was collected. Bees which had been placed in their hives only shortly before the beginning of the experiment, left the hive again regularly during the period of electrical field influence. On the other hand, bees which had already become used to their hives before the experiment began to seal up all crevices and holes with propolis, including the hive entrance. Lack of oxygen led to intensive wing-fluttering, causing a sharp rise in temperature and the eventual death of the insects.
> (Warnke, 1989a, pp. 82-83)

Highly sensitive swarms showed measurable reactions to field intensities of 100 V/m at frequencies between 30 and 40 Hz, whereby when the field was applied, all their wings suddenly began to flutter at a rate of 100-150 Hz.

Magnetic fields

The response of insects to magnetic fields, specifically the geomagnetic field, has been demonstrated repeatedly. Both the beetle, *Tenebrio*, and the sandhopper, *Talitrus saltator*, were found to orient to the earth's magnetic field in complete darkness (Arendse, 1978), while the beetle, *Melolontha vulgaris*, is strongly affected by magnetic fields (Schneider, 1975). The orientation of the bee dance on a vertical honeycomb is affected by very small experimentally induced alterations in the ambient magnetic field (Lindauer and Martin, 1968; Lindauer, 1972). Some evidence exists that ants may sense the geomagnetic field (Markl, 1962). Cockchafers, bees, crickets, wingless termites, and many flies were found capable of orienting to the geomagnetic field (Becker, 1963a,b). In particular, flies almost always land in an east-west or north-south direction with respect to magnetic north and irrespective of the sun's location. Resting flies maintain this direction or alter it by rapid 90° movements (Becker and Speck, 1964). One interesting result they found was that dead flies suspended on long threads reacted to magnetic fields as well. In reference to magnetic fields, this noted effect upon dead flies may very well be related to the behavior of live ones.

Becker found that in the field of a permanent magnet 100x stronger than the geomagnetic field, insects become excited, but after some time they orient themselves parallel or perpendicular to the magnetic lines of force. Very strong magnetic fields suppressed insect activity he found as Kisliuk and Ishay (1977) also discovered with the hornet, *Vespa orientalis*. These two researchers found that an additional horizontal magnetic field is lethal for adult hornets and larvae, but the juvenile hornets are capable of adapting, although not before they remained relatively motionless for 4 or 5 days. Kisliuk and Ishay (1977) showed that comb-building in *Vespa orientalis* is highest in regions of high-field intensity and progressively lower in regions of low-field intensity, while Martin and Lindauer (1973) found honeybees to respond to a 10-fold increase in the magnetic field by building cylindrical combs fastened to the floor rather than the roof.

A mechanism, or even a specific receptor mediating these responses to magnetic fields in insects was unknown. Bacteria had been found to contain intracytoplasmic membrane vesicles rich in iron (Blakemore, 1975) but it was not until 1978 that Gould and associates (Gould et al., 1978) discovered ferromagnetic particles, magnetite, in the honeybee abdomen. Later, Jones and McFadden (1982) discovered magnetic material in the body of the monarch butterfly. The earth's magnetic field is equivalent to 0.5 to 0.7 gauss (Zimmerman and Rogers, 1989), the variation due in part to the seasonal changes and particular location on the earth (Prolic and Nenadovic, 1995). Additionally, the vertical component of the earth's magnetic field has a greater magnitude than the horizontal (Blakemore, 1975). Honeybees can be trained to respond to very small changes in geomagnetic field intensity (Walker and Bitterman, 1989b). This sensitivity is suspected to aid in navigation when foraging away from the hive. Walker and Bitterman (1989a) also attached magnets to honeybees and successfully impaired magnetic field discrimination. Since these magnets were placed above the magnetite crystals on the abdomen, it was implied that these crystals may be involved in detecting the geomagnetic field.

The position of vertical galleries built by the termite, *Heterotermes indicola*, was found to be influenced by the weak alternating magnetic fields generated by the electric heater in an air-conditioned basement testing room (Becker, 1976b). Becker used earthed hardboard plates coated with silver paint thus excluding the electric field component (E), but allowing the magnetic field component (H) of an EM field to permeate the plate unhindered (Becker, 1976a). At a distance of about 2 m, the intensity of the alternating magnetic field was lower than 1 gamma (γ) and yet the termites could still detect the field from this distance. These results came after similar work which found feeding activity is influenced by disturbances in the geomagnetic field in a 27-day rhythm (Becker, 1976b; Becker and Gerisch, 1977) which correlated with the rotation of the sun as well as sunspot activity (Becker and Gerisch, 1973).

Unnaturally high levels of magnetism, higher than the geomagnetic field, are often utilized in biological research. Levengood (1967) concluded that *Drosophila* pupae subjected to high magnetic fields exhibited morphogenetic anomalies which were transmitted for 30 generations. Levengood (1965) and his coworker Shinkle (1962) observed an increase in the number of progeny per generation in periods of enhanced solar activity. The effect was more pronounced when the magnet was oriented with its north pole pointing east and the south pole west than when it was placed perpendicular to this direction. The effect was greater near the north pole than near the south. These experiments show the importance of a modulated magnetic field on insects, and in this case, involving fecundity. Magnetic storms would modulate any EM field in the environment and Cherneyshev (1966) showed a high correlation between insect activity to light traps and magnetic storms: The correlation coefficient was an astounding 0.926 after accounting for the usual factors, such as temperature, pressure, and humidity.

A permanent magnetic field of 320 millitesla (mT) which is about 10,000 x higher than the earth's field, was used in an adult emergence study involving the beetle, *Tenebrio molitor* (Prolic and Nenadovic, 1995). These investigators found that pupal metamorphosis into adults was more rapid in the presence of a magnetic field, resulting in a 14% reduction in eclosion time.

Generally however, high magnetic fields were found to have less effect upon organisms than low magnetic fields as reviewed in the book *Electromagnetic Fields and Life* by Presman (1970). One study involving insects showed that low levels of magnetic fields of 3000 to 4400 Oe (Oersteds) led to genetic changes in *Drosophila* (Mulay, 1964) while Reischer (1964) found that higher field strengths had no effect.

I have just mentioned that the termite, *Heterotermes indicola*, was discovered by Günther Becker to be influenced by the magnetic field produced by the hot water heater in his laboratory (Becker, 1989) which was 2 m away from the experimental set-up. This distance was not unprecedented since as long ago as 1900, Danilevskii (quoted in Presman, 1970) detected the excitation of a frog nerve situated at a distance of several meters from an EM source (a spark gap). Becker (1971) determined that these termites can build horizontal galleries that follow the main directions of the geomagnetic field, and that many insects including cockchafers, bees, crickets, wingless termites, and many flies are capable of such orientation as well (Becker, 1963a,b)

Termite biofields

External fields and their influence upon insects were discussed above. However, since all live animals produce an electromagnetic field, (some refer to this as an aura) the question of whether other animals are capable of detecting these fields is of profound scientific interest. These ultra-weak fields exist in the space proximal to a living organism (Zimmerman and Rogers, 1989) and extend outward in vanishingly small intensities to infinity (which is theoretically detectable assuming highly sensitive equipment is used). Sharks and their relatives and even the platypus detect extraordinarily faint electromagnetic fields that their animal prey produce (Gregory, 1991). An important question to ask is, "If detection is possible, will this information be used for communicating?"

Becker (1977a) has shown that termites are capable of detecting large numbers of their own by way of a physical field that is collectively produced by groups. He has named this physical field a "biofield". The larger the group, the greater the distance the effect is observed. The building of vertical galleries by termites is suppressed in the proximity of large groups of termites (Becker, 1976c, 1977b). He has explained the biofield as not stemming from any static electric fields, since the experiments were conducted under the naturally high humid conditions termites are generally found in. Instead, he suggested that these may be alternating electric fields (Becker, 1977b). This conclusion was apparently reached from two lines of evidence. The first is that termites can be directionally influenced by artificial alternating electric fields of low energy (Becker, 1977a) and secondly, by the work of Ulrich Warnke who only two years earlier demonstrated that alternating electric fields produced by flying bees are perceived by other individuals (Warnke, 1975). Direct evidence came for Becker when the effect was completely suppressed by the addition of 5-mm-thick aluminum plates, one of which was placed under all containers and the metal grounded (Becker, 1977a).

Groups of 500 individuals produced biofields detectable up to 4 cm away, thus inhibiting gallery building in the direction of the biofield (Becker, 1989). When 250 individual termites were tested, the response was very weak at 4 cm, but 500 termites showed no response to their own, when the distance was increased to 6 cm. The phenomenon that termites produce a larger biofield the larger the group suggests some form of synergism or interaction, and this interaction may very well be electromagnetic in nature since EM fields possess the property of falling off by a factor of four as the distance is doubled (inverse square law). Tunnel building at the periphery of a termite colony will help to expand the colony and thus improve resource gathering. The biological importance of detecting their own biofields so as not to build tunnels in the center of the colony but rather at the periphery most certainly is related to resource gathering (Becker, 1977b).

In order to test the strength of this response, experiments with competing variables were designed. The biofields produced by 750 or more termites are stronger than the alternating magnetic field produced by the electric heater in the room. The fields produced by 400 or less termites, however, are weaker than the magnetic field at a distance of about 2 m from its source, but slightly stronger at a distance of 4 m from the heater. Termites were found to respond to fields produced by species from other families of Isoptera, but not insects from even related orders, such as Blattaria (Blattoidea). Additionally, the reaction of termites to physical fields may only be observed when all other factors are carefully controlled (Becker, 1977c).

Many individuals with their own biofield may not add more energy to the group, only more units of energy. The intensity of energy from the group might remain the same. Additive effects may have something to do with their orientational ability. A correlate is found in most birds, especially the migratory species. Individual birds have relatively low orientational ability, while the power of the community in this respect is very high (Naumov and Il'ichev, 1965). These two researchers wrote "The community in this case frequently emerges as a mediator between the individual and various environmental factors, like a whole "organism" with interdependent interconnections." Both of these studies are examples of electromagnetic bio-information, and a fascinating book with the same title reviews and discusses the literature on this with wonderful insight (see list of references).

One of the strangest cases of electromagnetic communication possibly involving biofields also involves termites but of an unknown species. In 1937, Eugene Marais described a peculiar behavior of these termites in their underground home which was paraphrased by Callahan (1971)

> The cell of the queen termite was encircled by a ring of soldier termites. The soldiers were equally spaced; half standing on the floor of the queen's chamber in the area of a half circle facing the queen, and the remaining soldiers hung upside-down from the chamber roof around the other half of the circle. All their heads faced directly toward the magnetic north. Marais concluded that this formation was not a guard ring about the queen because he could not stir up the strange bodyguards to attack. What then was their function? While Marias was observing them, a large piece of clay fell from the roof of the queen cell and dealt the queen a hard blow; she began moving her head from side to side Immediately, the circle of bodyguards broke up and wandered around aimlessly. All the workers even in the most distant chambers of the colony, ceased work and swarmed into the palace cell. Soldiers and workers in the most remote parts of the colony gathered in excitement. Slowly the queen recovered, ceased the rhythmic movement of her head, and the colony returned to normal. The soldiers replaced themselves in a circle, and the workers in the remote chambers proceeded back to work. Marais concluded that the strange circle of soldiers was a link between the brain of the queen and the colony and carried the influence of the queen to all parts of the colony.

Magnetic field detection

The detection of magnetic fields by an organism is not completely understood, but this lack of knowledge has led to extremely innovative thinking in the development of hypotheses. Seven effects of magnetic fields on organisms were listed by Barnothy (1969) in her book *Biological Effects of Magnetic Fields* and they are:

1. The existence of transient free radicals which interact with the magnetic field.
2. A change in the rate or mechanism of diffusion across a membrane.
3. Semiconductor effects which would be influenced by the applied field.
4. A change in the rate of production of hormone secretion, for example, oxidative processes may be altered, influencing the oxidation rate of unsaturated steroids.
5. A distortion of the bond angles via paramagnetic molecules which change the fit between enzyme and substrate.
6. A change in rotational polarization of molecules with specific reactive sites.
7. A change in the rate of proton tunneling in DNA molecules caused by the applied magnetic field.

The majority of chemical reactions involve molecules, free radicals, and coenzymes, the latter being mostly bound to metals. Since these can change their character and direction in a magnetic field (Prolic and Nenadovic, 1995), the striking conclusion to be reached is that a magnetic field will influence almost any biochemical reaction.

Further, a magnetic field may be able to influence almost any physiological mechanism partially due to their strong dependence on biochemical reactions. An external magnetic field may be transmitted by the neuro-endocrine system, but indirectly so. The data obtained by Blackmann (1994), along with his colleague, Most, in 1993, indicated that the information may start with the Ca^{2+} ion, at the neural cell membranes. The calcium ion in turn regulates the secretion of neural hormones reaching the effector glands and tissues via neurosecretory pathways. The influence of the magnetic field then would have indirectly influenced many different sites in the body.

The two simplest and most straightforward theories as to how animals detect magnetic fields were given by Jungerman and Rosenblum in 1980. They are the mechanical detection of a torque on a magnetic material or the detection of an electromotive force generated in a moving conductor (i.e. the neuron). The latter is called "magnetic induction". Based upon theory alone, these two researchers concluded that a magnetic detection system using induction is unlikely for animals in flight.

The detection of weak magnetic fields has long been a mystery to scientists. How animals can orient to the geomagnetic field, at only 0.5 gauss, is amazing in and of itself. (This fact finds particular fascination in man, since we have no conscious awareness of the earth's magnetic field.) However, modulating the geomagnetic field can help make both the field and the modulating wave more easily detectable. According to measurements taken by Cohen (1975) the strongest magnetic fields from the human body emanate from the heart, and these fluctuating fields measure only 1×10^{-6} gauss in normal subjects. Some very large biomagnetic fields are created by unnatural circumstances such as lung contaminants which are still about 50,000 x weaker than the geomagnetic field (Zimmerman and Rogers, 1989). Can insects respond to these low level magnetic fields? If there is sufficient time to carry out a special analysis on a signal, it is at least technically possible for man to recover signals with a level far below the interference limit (Kõnig, 1989). A comparable situation is also conceivable from the perspective of a biological organism. Ulrich Warnke has studied for years the effects of alternating magnetic fields upon humans and has obtained results suggesting that effects may be observed by forces as much as 8 levels of magnitude lower than forces caused by thermic noise (Warnke, 1989b).

By and large, biomagnetic experiments, especially involving low-level fields, indicate that the biological effect of the magnetic field is not instantaneous, but requires a continuous exposure to the magnetic field for a critical length of time in order for the effect to be observed (Abler, 1969). This strongly suggests that neuronal spikes do not occur in quick response to field exposure, and that electrophysiological techniques would not be very useful in measuring a response of this type.

Even though some interaction probably exists between the CNS and external magnetic fields (Becker, 1969), the effect is likely not on the action potential since no effect on a variety of action potential parameters occurred with exposure to high strength fields (Liberman et al., 1959). Instead of the usual increase in spike (action potential) rate, Russell (1969) reported a 17-27% inhibition in firing rates in the subesophageal ganglion of the cockroach, *Periplaneta americana*, when exposed to a constant magnetic field of 6600 Oe.

Most of the established biomagnetic effects have been observed *in vivo*. Since very small energy is imparted on a biological system by a magnetic field, it seems likely that a built-in amplification system may occur in the organism (Barnothy, 1969). Smith (1989) and Kroy (1989) reported the possibility that the entire organism may be responding to the magnetic field, or the total mass of the connective tissue, and not just a part of the organism. Since all organisms have an electromagnetic aura about them, a magnetic field would certainly affect this aura. If the aura were affected, either good or bad, then there is always the possibility that the organism may be able to detect the magnetic field simply by virtue of its interaction upon the homeostatic mechanisms, which collectively contribute to a healthy aura. Therefore, if the electrostatic charges of an animal, especially a flying animal, come into a complex interaction with the terrestrial magnetic field (a much greater field intensity), and if the resulting nuances are of use to the animal, then magnetic field orientation can occur (Warnke, 1989a). A special magnetic sense would thus be rendered unnecessary.

Magnetic fields, unlike electrical fields, are able to penetrate deeply into biological tissue. Electrical currents have difficulty in passing through the relatively low-conductivity (human) skull, whereas magnetic fields do so easily (Zimmerman and Rogers, 1989). For this reason, any magnetic receptors, if present, need not be located on the outside of the body (Warnke and Popp, 1989). The central nervous system of humans is predominantly internal and can be influenced by magnetic fields with frequencies of extremely narrow bandwidths (1.6-3.6, 7.8, 10.8, 11.4 Hz) and low amplitudes (Maxey, 1975).

The phenomena that all fish are surrounded by individual electromagnetic auras is well known. These auras take on the form of a dipolar continuous current field, where the mouth is negative and the gills are largely positive. This EM field is modulated by mechanical breathing. This modulated field is easily detectable to sharks, rays, and sturgeons, as signs of prey. Discrete receptors are implicated in this case, and they are called the "ampullae of Lorenzini".

Identifiable receptors exist in some organisms, as I have already discussed with the bacteria and honeybees. However, one cannot assume that these receptors will react and convert the message in the same way. Bacteria responsive to the geomagnetic field contain novel structured particles, rich in iron, within intracytoplasmic membrane vesicles (Blakemore, 1975). The honeybees, on the other hand, contain magnetite in their abdomen (Gould et al., 1978). Although both iron and magnetite do respond to magnetic fields, the system in bacteria is likely different from that in honeybees since the physical make-up of the receptors differs as well as the magnetic substance utilized.

Ferritin, a protein complex of iron, contains about 23% by weight of the elemental metal (Senftle and Hambright, 1969) and is relatively paramagnetic (a weak attraction toward a magnet). It plays an important function in both plants and animals (Neurath, 1969), however, it is not known whether or not this ubiquitous substance plays a role in insects. If ferritin were found to occur in insects, then one would almost certainly expect this molecule to be associated with some sort of magnetic reception.

The detection of magnetic fields may also be detectable by the use of modulated waves similar to what I have discussed several times already. A magnetic field that influences another may in turn influence the insect that is capable of detecting the carrier wave (the wave being modulated). For example, *Drosophila* grown in magnetic fields demonstrated an inverse relationship between solar flare activity (a magnetic effect produced by our sun) and their progeny yields (Levengood, 1962; 1965).

Since magnetic fields may sometimes only be detected by their effect upon other magnetic fields, the environment in which one conducts magnetic research should be carefully analyzed so that a researcher will be aware of stray electromagnetic fields and maybe even control them, if possible. The magnetic field in a normal laboratory is generally a combination of the geomagnetic field and the stray fields produce by nearby AC or DC electric currents, rotating machinery, or magnetic devices. Magnetic field intensities ranging from ½ gauss (G) to 100 G or more are often measured at various locations in a laboratory. Both the magnitude and direction of the field can be significantly affected by the movement of large metal objects in the room, switching of electric power, and other normal laboratory activities (Abler, 1969).

Household electrical fittings must not go unmentioned in this discussion, for their different ways of functioning can lead to considerable variations in field intensity values from room to room. Wires not shielded in metal tubes and installed in walls have proven especially unfavorable in this respect, since they produce relatively intense electric fields in their vicinity at a frequency of 50 or 60 Hz (König, 1989). It is particularly difficult to measure signals in the general environment with frequencies below 100 Hz due to interferences of technical origin; for example, the 50 or 60 Hz power current, the 16 2/3 Hz railway current frequency, and the 25 Hz telephone ringing signal, whose intensity is usually far above that of fields of natural origin (König, 1989). This potential noise must be suppressed in an animal by means of a suitable filtering technique, which may or may not be occurring at the organismic level.

The positive effect of magnetic fields upon insects may not all be involved with *detection* so much as it may be for *protection*. Amer and Tobias (1965) found that the percentage of morphological changes in the wing of the flour beetle, *Tribolium confusum*, due to ionizing radiation is reduced if a magnetic field of 8000 G is applied at the same time. This curious finding may be complex since the protective effect depended on temperature and on the partial pressure of oxygen, and the authors believed hormonal regulation to be affected.

The detection of electromagnetic energy by insects in many cases is very difficult over great distances. This is due to the inverse square law which states that "the intensity of radiation emitted from a point source varies as the inverse square of the distance between the source and the receiver." For this reason, EM radiation falls off substantially from its source over greater and greater distances. However, one possibility of still detecting EM radiation from insects great distances away, is by moving the source of EM radiation closer to the receiver. Even if the insect is immobile, this can be accomplished by releasing substances into the atmosphere which themselves give off an electromagnetic message. This EM message can then be received directly from the airborne substances and only indirectly from the emitting insect.

Molecular emissions

Molecules that are above 0° Kelvin are resonating and both absorb and emit electromagnetic energy. These resonations have to do with bond lengths. All bonds stretch, bend, lengthen and contract (McMurry, 1988). Thus a typical C-H bond even at relatively cool temperatures, is actually vibrating at a certain frequency, alternatively stretching and compressing. When the molecule is irradiated with electromagnetic radiation, the vibrating bond will absorb energy only if the frequencies of the light and the vibration are the same.

Infrared spectrophotometers are designed to expose organic molecules to infrared energy in order to observe what wavelengths are absorbed or emitted and to what degree. The infrared spectrophotometer especially assists the organic chemist in determining what type of bonds the molecule contains, as well as the types of functional groups present. An infrared spectrum contains dozens and maybe hundreds of emissions or, usually absorptions (recorded on a printout as absorption or emission lines) that all contribute, in their own way to the structure determination of the molecule. Each molecule has its own "fingerprint". The wavelengths absorbed are specific for each molecule, and many of these absorptions give clues to the shape and arrangement of atoms in a particular molecule. Near-IR and intermediate-IR radiation are associated with resonances in molecular bonds as well as blackbody radiations produced from heated materials. Far-IR radiation is usually associated with rotational vibration of larger molecules (Hsiao, 1972).

A molecule cannot absorb unlimited amounts of energy. Sooner or later, all the absorbed energy must be released and these emissions may be detected. As early as 1965, physical chemists were utilizing multiple-scan interferometry to characterize organic compounds by means of their self-emitted infrared radiation (Low et al., 1965), even though IR spectroscopy was invented by John Tyndall about one hundred years earlier (Tyndall, 1866). The absorption of energy by atoms, molecules, free radicals, or ions can produce excited species, decomposition, or ionization. A minimum energy, and often a specific frequency is required for each type of reaction.

Some molecules do absorb in the visible or ultraviolet (UV) range and are converted into more highly toxic molecules. The introduction of these molecules, which are dyes, to insect infestations so that consumption of the relatively harmless molecule occurs thus allows for a delayed toxicity. Once the insects are exposed to sunlight, visible and UV radiation sensitize the ingested molecule, eventually killing the insect outright (Heitz, 1987).

These type of molecular reactions are not what I wish to discuss now, although the process is similar.

Most molecules with which insects communicate on a regular basis are not known to change forms upon absorption of radiation. Instead, the radiation is simply absorbed only to be emitted soon after. A common household use for this physical phenomena concerns the laundry. Optical brighteners are used commonly in soaps, detergents, and fabric softeners. These compounds absorb UV energy and convert it to visible light (Villaume, 1958). Curiously, optical brighteners have also been utilized to enhance viral activity against the gypsy moth (Shapiro and Dougherty, 1994).

Wright advanced the theory that low-frequency molecular vibrations or rotations provide the physical basis of odor (Wright, 1954). Philip Callahan has put forward the hypothesis that insects are able to detect these molecular emissions (which lie in the infrared), with sensilla functioning as dielectric waveguides. If insects do perceive these infrared wavelengths, this would enable an insect to identify a molecule precisely. By studying over 10,000 spectra from such molecules as plant hormones, pheromones, and plant scents (Callahan, 1990), Callahan found these emissions to possess nonlinear, coherent characteristics. This meant that the emissions are related to "lasers" These molecules could be pumped with certain types of radiation, which would stimulate them to emit coherent radiation. Coherent radiation, in turn, is more easily detected by tuned receptors below noise levels.

Extremely low frequency (ELF) radio frequencies have been shown by Koemel and Callahan (1994) to pump (put energy into) insects semiochemicals. These semiochemicals were stimulated by both phonon (sound) and photon (radio) ELF energy that pumps the semiochemical and raises its energy level to the point that it emits narrow-band (meaning coherent) infrared frequencies. These narrow-band infrared frequencies can be modulated just like any other frequency. If the insect has a wingbeat frequency of 50-60 Hz, then various light sources will reflect off the highly reflective exoskeleton and therefore modulate any incoming frequency, whether it be a molecular emission or otherwise (Callahan, 1990).

Lepidoptera and Odonata have relatively low wingbeat frequencies, as do green lacewings (Chrysopidae), and some beetles. All these insects are commonly attracted to flickering (60 Hz) light. One would then anticipate insects with a quicker wingbeat frequency to be attracted not toward 60 Hz but rather a 200 or 300 Hz frequency. The only source I could find in the literature involved the tsetse fly (Griffiths and Brady, 1994). This study reviewed the literature and found that standard electric nets caught less than half of the tsetse flies that approached them. These two English researchers designed a similar type net that killed a modest 55% of the tsetse flies that approached when the electric net was used at a 50 Hz operating frequency. However, when the spark frequency was increased to 200 Hz, the trap killed 88% of the flies that approached. The kill rate was a direct result of higher attractancy, in the sense that flies were enticed to more closely approach the electric grid.

Insects may actively modulate other incoming EM messages in addition to those related to wingbeat frequencies. Antennae from noctuid moths such as the cabbage looper, the corn earworm, the fall armyworm, and the american cockroach all continuously vibrate their antennae at 60 Hz when exposed to a 60 Hz electric field (Mankin, 1976). Excised antennae sometimes vibrate, but other times did not, which suggests that the insect may be actively modulating the atmosphere immediately surrounding the antennae.

Pumping radiation can potentially come from anywhere, and both photons and phonons (sound frequencies) have been successfully used to modulate insect scents thus obtaining IR nonlinear emissions (Callahan et al., 1985). Vibrating antennae can modulate and stimulate molecules to emit. Insects from all groups are known to vibrate their antennae at specific frequencies. Callahan (1975b) spread a monolayer of cabbage looper pheromone in some wax and measured the emissions emanating from this layer. With the addition of a 50 Hz vibrating frequency the coherent emissions increased ten-fold. Cabbage loopers both vibrate their antennae and their wings at about 50 Hz. Numerous researchers have placed excised moth antennae in modeling clay, hooked up an electrode to the antennae, and subsequently measured the response. in terms of neuron spikes from the antennal nerve. These spikes are measured in response to various odors that pass across the antenna. Assumedly, these experiments are all carried out with the alternating 60 Hz field produced by the electrophysiological apparatus as well as the 60 Hz pumping frequency from the room lights. It may be that these artificial frequencies substitute for the natural frequencies (antennal vibrations) that are certainly absent in an excised antenna.

Different types of molecular emissions are given various names. Photoluminescence is the condition whereby molecules are excited to radiate by interaction with photons of light. Two types of photoluminescence are triboluminescence, where light energy is emitted by breaking or rubbing certain organic molecules, and chemiluminescence, where the emitted energy is produced by a chemical reaction. Two additional types of photoluminescence are phospholuminescence and fluorescence where energy release is delayed or immediate, respectively.

Three varieties of fluorescence include Stokes fluorescence, where the re-emission of less energetic photons which are of longer wavelengths than the absorbed photons occurs; anti-Stokes fluorescence, where re-emission of less energetic photons occurs which are of shorter wavelengths; and finally resonance fluorescence, where re-emission of photons possessing the same energy as the absorbed photons occurs. Usually the release of energy from an atom or molecule will be of a longer wavelength than the absorbed energy or pumping radiation. Drexhage (1970) has reported that when an excited dye molecule emits light by the process of fluorescence, its behavior is remarkably analogous to that of an antenna emitting radio waves.

Molecules emit and absorb photons of specific frequencies, and within certain regions only certain energy changes are possible. Many long-chain organic molecules absorb and emit in the intermediate and far infrared from 2.5 to 400 µm. The lengths of insect sensilla commonly attain 300 µm. This means that insect sensilla are within the range, more or less, of 2 to 6 wavelengths, the optimum length given for a tapering dielectric waveguide (Kiely, 1953).

Infrared spectra for gases contain much narrower bandwidths than those same molecules in the liquid state. This fact would suggest that olfaction (smell) is more precise than gustation (taste). Nothing in the literature seems to refute this.

One important piece of research further supporting this involves the infamous lovebug, *Plecia nearctica*, of the southeastern United States. Lovebugs are highly attracted to often traveled roadways during daylight hours (10 am to 4 pm). The exhaust fumes produced from automobiles on the highways were collectively implicated as the attractant molecules, but the exhaust fumes were not found to be attractive to the lovebugs to any significant degree (13% attraction) (Callahan and Denmark, 1973). They assumed that the pumping frequency was missing, and surmised that , because their experiments were conducted indoors, ultraviolet energy from the sun may be required. Since ultraviolet radiation from the sun does not penetrate the atmosphere below 330 nm, a pumping frequency of 360 nm was chosen.

Although the lovebugs showed little attraction to the UV radiation alone (10%), when the exhaust fumes were combined with the UV radiation the lovebugs' response toward the source occurred instantaneously and to a very high degree (92.8% attraction). The only insects that failed to respond within 1 to 10 seconds were either injured or moribund. When these two researchers repeated the experiment 12 years later, the attractant response attained 100% (Callahan et al., 1985). Response to the attractant and the speed of the reaction were the greatest ever witnessed by the authors. The lovebugs also flew either upwind or downwind to this source. Furthermore, low light intensities, below that which would stimulate flight, caused the insects to crawl toward the attractant. Obviously, some sort of synergistic interaction between the two stimuli must be occurring.

In another experiment Callahan placed corn earworm moths in a blackened cage with a corn plant in which to oviposit (Callahan, 1957). If the moths were attracted to the scent alone emanting from the corn plant than the plant should be the primary site for oviposition. However, 98% of the eggs were oviposited on a piece of cloth placed opposite the plant with blue light shining on it. The corn plant obviously has the higher concentrations of corn plant scent molecules about it, but very few "hot" molecules (molecules pumped up by the blue light and emitting coherently). The other side of the blackened cage contained a lower concentration of corn scent molecules, but many more "hot" molecules, pumped by the blue light (Callahan, 1997). If insects do indeed follow the concentration gradient of molecules toward a point source, such as another moth or a plant to oviposit upon, then virtually all of the eggs should have been oviposited upon the corn plant, yet this did not occur.

Many pheromones have been isolated from insects, synthesized, and then released into the environment from a point source, such as a trap, in an effort to attract noxious species. Little success has been achieved by this method, possibly because the molecule is simply released into the atmosphere with no thought to pumping frequencies nor the molecular emissions emanating from it. I have mentioned UV light as an important pumping frequency for the molecules from car exhausts that attract lovebugs so readily. Entomologists have long used blacklights (a UV source) to attract insects. Often they use them as an index for calculating population densities of certain species within an area. The prevailing thought among many is that blacklights alone are the main attractant.

One of the insects for which a blacklight is currently used for population studies is the gypsy moth, *Lymantria dispar*. Wallner and colleagues (1995) have recently shown that the gypsy moth, as well as two of its relatives in the same family, Lymantriidae, are more highly attracted to fluorescent blacklight lamps than either phosphor mercury or high pressure sodium lamps, but both of these latter sources were unattractive to all three moths after the addition of filters that blocked spectral emissions below 480 nm (blue/violet and ultraviolet).

The common explanation for this phenomenon is that the moths are visually attracted to the blacklight, to which we know many insects have sensitive pigments. Most researchers I know assume that the moths are attracted to visible and ultraviolet light via visual perception through the compound eye. Hsiao and Hackwell (1970) concluded that the compound eye is the only sensory detector which mediates the attraction to visible light. However, Brown and Cameron (1977) have shown that gypsy moth males, who show a very strong attraction to ultraviolet, do not contain photosensitive pigments for this spectral region. In fact females were shown to reflect UV quite readily from their ommatidia.

When the compound eye of *Coccinella septempunctata* was found to have pigments photosensitive to 365 and 500 nm, the conclusion reached was that these two electromagnetic frequencies (UV and green, respectively) must be the most important wavelengths for the behavior of this species (Agee et al., 1990). The same conclusion can be drawn for the gypsy moth, in the sense that EM frequencies not readily perceived by the eye are probably not visually important to the gypsy moth's behavior. Apparently, the gypsy moth's strong attraction toward UV light is through some other modality than the visual system, that is the compound eye and ocelli. Could the UV light instead be a pumping frequency for attractant molecules?

The cabbage looper pheromone, when used in conjunction with a black light trap, increased the capture rate from 6 to 10x over either stimulus alone (Henneberry and Howland., 1966b; McLaughlin et al., 1974). Blacklights baited with virgin females caught 20-30 times the number of male moths than unbaited blacklight traps (Henneberry and Howland, 1966a; Henneberry et al., 1967a). Significantly higher catches of tobacco hornworm males occurred when female moths were used in conjunction with blacklight (Hoffman et al., 1966; McFadden and Lam, 1968).

Some interaction between the pheromone and the blacklight, presumably the ultraviolet energy, is likely occurring, especially considering that a blacklight situated 20 ft. from a baited trap caught 10-15 times more cabbage looper males than blacklight traps situated one mile from the baited traps (Henneberry and Howland, 1966a). A relative close proximity to one another was apparently necessary, which makes sense if indeed the energy and the molecule are interacting. Hoffman and colleagues (1966) reported a critical observation supporting this when they noticed that the males of the tobacco hornworm who approached light traps did not seek out the virgin females; instead, they reacted primarily to the blacklight. Much like the corn earworm experiments conducted by Callahan (1957) already mentioned, the "hottest" molecules will be located near the blacklight.

The supposed attraction of moths to high intensity light is another popular misconception in entomological circles despite the well-published inability of many researchers to increase the trap catch proportionally by increasing the intensity of light (Taylor et al., 1951; Glick et al., 1956; Deay et al., 1965; Hollingsworth et al., 1968; Lam et al., 1968). Besides, this did not seem to explain the reason why moths are so attracted to the very low light produced from burning candles. Callahan (1969) has hypothesized this to be an attraction to the pumped hydrocarbon molecules that are released from the burning wax. Two earlier works seem to support this hypothesis. Sparks and colleagues (1967) captured a substantial number of moths with an oil-filled pan (a pan full of hydrocarbons) below a light source, while Hartstack and colleagues (1968) caught moths in oil-filled pans placed on the ground surrounding a blacklight. Many of the pheromones that have been isolated from moths have hydrocarbon backbones.

Certainly, all pumping frequencies need not be equivalent. Cylindrical electric grid traps baited with synthetic pheromone of the cabbage looper caught 6-7 times more males than a similarly baited can trap developed specifically for this insect (Mitchell et al., 1972). Here the pumping frequency was apparently a 60 Hz alternating electric field. Success has also been obtained with grid traps for cabbage looper males by other researchers also (Toba et al., 1969; Kishaba et al., 1970). Similarly, grid traps baited with virgin female tobacco hornworms, *Manduca sexta*, were 2-9 times more effective in trapping males than a screenwire pheromone trap designed for this purpose (Mitchell et al., 1972). Since either the pheromone or the moth were both effective lures in conjunction with the electric traps, one may conclude that the electrical effect may just be affecting the pheromone and not the insect herself.

Pickens and Thimijan (1986) showed that a Beltsville trap placed inside of a black box at a manure dump and illuminated by a 40-W blacklight bulb caught 15,117 flies over 19 days, while a similar trap and bulb without a darkening box and placed 4 m away caught only 10 flies in the same period.

If there is sufficiently high concentration of pheromone in the atmosphere, pumping frequencies will be pumping atmospheric molecules more readily than if there are low concentrations. Campbell and colleagues (1992) have recently reported that blacklight traps capture more corn earworm moths than pheromone traps later in the season when populations were at their highest. When populations were low, pheromone traps caught more. Because the pheromone is really the primary attractant and not the blacklight, the efficacy of the blacklight is irreversibly dependent upon the molecule in order to work effectively. Sparse molecules render the blacklight only "a solitary beacon in the cool night", while high concentrations of molecules transform the blacklight into "a raging inferno", uncontrollably attractive to the helpless moth.

Since several types of pumping frequencies appear to increase the attractiveness of various insect semiochemicals, Callahan and Hamilton (1977) stimulated the cabbage looper pheromone with a blacklight bulb (UV source) as well as a 50-60 Hz frequency from a stroboscope (Callahan, 1977a) to simulate the moth's wingbeat frequency. Much stronger emissions did indeed occur from the pheromone when analyzed on a spectrophotometer.

If indeed the insects were attracted to the molecular emissions produced by organic compounds, then some sort of attraction must exist toward a pure electromagnetic message. Separating the molecule from its own emission is a tricky thing, since producing the right "fingerprint" would necessarily involve producing many infrared emissions, thus simulating the natural IR fingerprint that so wonderfully identifies the molecule and separates it from all others.

Diesendorf and his colleagues (1974) have pointed out some unexplained experimental results which seem to support Callahan's hypothesis that insects do respond to the molecular emissions emanating from molecules. Kafka (1972) revealed that the effectiveness of methylated compounds depends largely on the energy levels of intromolecular rotations. That same year, Hummel and colleagues (1972) showed that a deuterated form of the parapheromone loop-lure is 50% less attractive to the cabbage looper male than the undeuterated form. Deuteration does not change the structure of the molecule in any way, however, the heavy hydrogen does alter the vibration frequencies of the molecule itself thus altering the molecular emissions.

Wright and Brand (1972) have reported a high correlation of ant alarm pheromone activity with molecular emissions in the infrared. Their technique was innovative. Both researchers searched for molecules that contained similar infrared spectra (molecular emissions) to that of the ant pheromone, 2-heptanone. They found nine candidates and simply tested them on the ant, *Iridomyrmex pruinosus*, in order to observe how similar the ant's behavior was relative to the ant pheromone. Incredibly, seven of the nine compounds gave a distinct behavioral response, even though their structures were in no way related to 2-heptanone. They commented, "A correlation of pheromone activity with the shape of 2-heptanone seems to be wholly incapable of accommodating, not to mention predicting, the alarm pheromone activity to such substances as triethyl amine, heptyl butyrate or terpineol acetate."

One year before this, Wright was able to demonstrate that 12 structurally unrelated compounds had similar odors to a "green" plant-like odor when tested on experienced perfumers (Wright, 1971a). These compounds although structurally unrelated to the "template" compound were perceived in similar fashion by humans. These twelve compounds were chosen based solely upon their similarity of possessing three infrared bands, or windows, in relation to the template compound. These three bands displayed windows between 215-234 μm, 275-294 μm, and 300-319 μm.

These two studies correlated certain bands with olfaction in both humans and insects but another interesting result came from these as well as two additional papers by Wright and colleagues (Wright, 1971b; Wright et al., 1971). These papers convincingly showed that infrared bands within a critical window display adverse behavioral responses. Molecules containing infrared spectra within a given band designated adverse, may diminish if not even abolish the attractant property of an attractant molecule. These infrared frequencies were termed "adverse frequencies" and their presence in a molecule labelled the molecule as an "anti-attractant" (Wright et al., 1971).

Wright has shown strong evidence for insects responding to molecular infrared emissions by successfully predicting that a "green" type of odor could elicit a response on the basis of infrared spectra (Wright, 1971a, Wright and Brand, 1972), by predicting that a wasp attractant could come from saturated and aromatic esters (Wright, 1969) when all previously known wasp attractants were unsaturated aliphatic esters (Davis, 1968), and finally the prediction of a repellency effect when certain substances, not themselves repellent, were added to known insect lures (Wright et al., 1971).

Related to this, deterrent receptors of several lepidopteran larvae have been investigated by electrophysiological methods. The single receptor cell responds to a variety of deterrents with drastically different chemical structures (Ma, 1972; Schoonhoven, 1972). Although infrared spectra from these molecules was not the point of investigation for these researchers, it would be interesting to see how related, if at all, the infrared emissions were from these deterrent molecules. The studies aforementioned seem to have enormous implications for future insect attractants and repellents.

CHAPTER 3
LITERATURE REVIEW 2- FLEAS

Ecology of Fleas

Fleas are a group of insects that belong to the Order Siphonaptera. The root name, "*siphon*", refers to its siphoning mouthparts; the following "*a*" denotes "not, or without"; and the "*pter*" ending means wing. Literally then, this is a group of insects with sucking mouthparts and no wings. The fossil record, as well as internal anatomy studies, indicate that the flea had wings at some point in its past, but for some reason, has secondarily lost them. All flea species today lack wings. Their primary mode of locomotion consists of an incredible leap produced from their hind legs, assisted by powerful leg muscles and a proteinaceous tissue known as resilin.

The order Siphonaptera consists of some 2500 species and subspecies (Pilgrim, 1991a) and is a holometabolous insect, which means fleas undergo a complete metamorphosis during their life cycle. Much like the order Diptera (true flies), immature flea larvae are called "maggots". They are legless, eyeless, worm-like creatures with a voracious appetite so indicative of virtually all holometabolous larvae whose main purpose in life is to feed and to grow.

Adult fleas are known vectors of some particularly horrible human diseases, such as the "black plague" (Pollitzer, 1960) and murine typhus (Farhang-Azad and Traub, 1985), as well as pruritus and dermatitis on domestic animals which is caused by their biting (Kissilett, 1938). Their vectoring role in transmitting organisms like the dog tapeworm, *Dipylidium caninum* is well known (Hamrick et al., 1983). Plenty of research has been conducted on adult flea behavior. However, comparatively little, well, virtually nothing, has been reported on the behavior of flea larvae.

Flea larvae are known to feed on the fecal droppings from the adult fleas who in turn are feeding on the host. Therefore, flea larvae are usually found associated with the host due to their indirect feeding association with the host. Some common flea hosts include cats, dogs, squirrels, birds and rats. Since the adult fleas feed on blood from the host, and the blood passes through the flea's digestive system relatively unchanged, a very nutritious blood-like by-product passes out of the adult flea for the benefit of their young. The fecal material dries and drops off the pelage of the host, where it is eventually consumed by the larvae who rummage through the nest litter and debris of the host. The nutrients found in the adult feces are not always necessary for successful development, since Bruce (1948) has reported that other organic material in the soil can be utilized for larval development.

Flea larvae usually have 3 instars, and are active scavengers living non-parasitically in nest debris of the host (Pilgrim, 1991a). Larvae range from 1.5-10 mm in length, and possess relatively small antennae, relative to most other insects, on a well-sclerotized head. As I have mentioned, they are legless and eyeless. Even the adult cat flea is not thought to have acute form vision (Rothschild and Clay, 1952) so if vision is not all that good in the adults who do have eyes, then just how good can it be in larvae that do not have any eyes?

Their only strikingly obvious sensory structures are the wonderful arrays of spines, stemming from all of their body segments. The sensory hairs so prevalent on the body are used extensively by flea systematists in separating and identifying fleas (Pilgrim, 1988). This taxonomic tool has been termed “chaetotaxy” (literally “hair taxonomy”). These sensory hairs are a characteristic of all free-living flea larvae (Williams, 1986).

These sensory hairs are thought to assist the flea larvae in crawling (Bushopp, 1915), however, the larvae crawl on their ventral surface where there are no setae. The setae stem from the lateral and dorsal surfaces only. The ventral setae on earthworms are apparently used for locomotion because of their position, and because they are short and thick, do provide a firm grip as it crawls over the substrate. The setae on flea larvae are long and thin and bend easily at their base. It is not likely that they are strong enough to be used as a support or brace for locomotion. Many other maggots, such as the house fly, do not possess body setae, and they have no trouble crawling around.

Body setae as a defensive structure is also an unlikely possibility since the setae are so “flimsy” and predators, such as fire ants, attack flea larvae with no trouble whatsoever. Besides, if these setae were important defensive structures, then house fly larvae might have them for protection from their many natural predators (Geden et al., 1988).

Earlier in this review I listed ten types of sensilla on insects by Zachurak and Shields (1991). The enormous number of insect species may help to explain the incredible number, but even flea larvae have a wide variety of morphologically distinct sensilla. In the same year, Pilgrim (1991a) described and separated nine different types of setae on flea larvae. He has listed them into two major categories of smooth and highly structured setae.

Smooth setae

-*acicular*- tapering to a fine tip (majority)
-*obtuse*- much stouter with blunt tip (Hystrichopsyllidae, Pygiopsyllidae) can be short (Hystrichopsylla s.l.) or very long (Notiopsylla)
-*attenuate*- narrowing to filament at about midlength (Chiastapsylla head capsule)
-*capitate*- swollen at tip. (all body setae of Ischnopsyllidae)
-*spatulate*- terminal swelling gradually developing from shaft (both capitate and spatulate are thin-walled)

Highly structured setae

-*branched*- spine-like process irregularly arranged (Pygiopsylla)
-*spiculate*- series of finer processes along one side of shaft (mostly Pygiopsyllidae but also in Chiastopsylla, Ischnopsyllidae)
-*pilose*- processes densely clothe the shaft
-*striated*- helically wound series of fine grooves (only Rhopalopsyllus)

Many flea larvae have only acicular setae, which may range in length from just a few micrometers to over 1.5 cm, but others may have in addition serrate, pilose, attenuated, spiculate, branched, or helically-striate setae; while in all Ischnopsyllidae that Pilgrim (1991b) examined many of the longer body setae are capitate, ending in swollen bladder-like tips of unknown function.

A sensillum of apparently similar design is found on *Melanophila acuminata*, the beetle discussed earlier as being attracted to forest fires. Its infrared sensory organ is composed of a pit, and located at the bottom of this pit are many closely spaced sensilla, each ending in swollen bladder-like tips of unknown function (Fig. 2-5e). Since this organ has already been identified as an infrared sensing device (Evans, 1964; 1966a), and the only sensilla present in the organ are semi-capitate in the sense that they are domed but lack a stalk (Evans, 1966b), it may be that the Ischnopsyllids use them for electromagnetic detection as well. The exact wavelengths received cannot be determined without making a model and testing the adjusted wavelengths, or mathematically by obtaining the proper dimensions of the sensilla and utilizing advanced calculus. From a behavioral perspective, ablation studies or even neurophysiology may shed light on this interesting organ.

The setal arrangement may be related to lifestyles as well, since flea larvae from the family Spilopsyllinae who parasitize birds have a different setal arrangement than those Spilopsyllinae who parasitize mammals (Pilgrim, 1991b).

One very interesting exception to all of the aforementioned flea larvae is *Uropsylla tasmanica*, which is the only flea known to have an endoparasitic larval stage (Williams, 1986). Larvae occur as sub-dermal parasites of dasyurid hosts such as Tiger cats, as well as the host by which the flea was specifically named after, the Tasmanian devil, *Sarcophilus harrisi*. Eggs are glued to the hair of the host wherein the newly hatched larvae burrow into the skin in order to feed and develop (Dunnet, 1970). Some hosts died of infestation while others were partly paralyzed when the shoulders were infested (Williams, 1986). This strongly suggests that parasitism is not a relatively recent development since host survival is key to a successful host/parasite relationship.

Another factor pointing to the possibility that this parasitic relationship is still in its infancy is the requirement of *Uropsylla tasmanica* to undergo four larval instars (Pearse, 1981). It may be that an additional instar above the more normal "three" is necessary due to poor nutritional quality of the food source, or in turn reflects an apparent inability to assimilate the food. A third factor is the retention of hairs in the first instar. Their subsequent absence in remaining instars appears to suggest their "phasing out" in this species. This brings up the question of their presence on other species, and the incredible importance fleas must hold them in since hairs are found on virtually all flea larvae of the world (Pilgrim, pers. comm.[1]).

The sticktight flea, *Echidnophaga gallinacea*, is a stationary ectoparasite anchored by its mouth parts to the host's skin (Harwood and James, 1979). Its larval stage is characterized by a noticeable reduction in the length of hairs found all over its body in relation to other species of flea. Even though the hairs are present and on all instars, they are severely reduced. This characteristic is also found on other species of *Echidnophaga* as well (Pilgrim, pers. comm[1].). This flea is sometimes known as the "hen flea" because of its dependence on penned chickens. There are other species of flea that parasitize chickens, but *Echidnophaga gallinacea* is only successful on penned chickens.

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[1] Personal correspondence by letter dated August 28, 1995.

> The sticktight flea, *Echidnophaga gallinacea*, is found predominantly among domestic chickens that are confined. They are not as common among domestic chickens that are allowed to roam over a wide range. (Hogsette, pers. comm.[2])

Among Siphonaptera, a considerable number of species spend the longest part of their life cycle in nests or burrows (Balashov, 1984). About 94% of adult fleas are primarily ectoparasites of mammals (Marshall, 1981). After attaching to a host, the sticktight fleas (*Echidnophaga, Vermipsilla, Dorcadia*) do not leave until the end of their life cycle or the end of their host's life cycle. The most specialized stage among fleas is the intradermal parasitism found in adults of the genus *Tunga*, and in the larvae of *Uropsylla tasmanica*. Most hematophagous arthropods are confined to a narrow range of hosts (Balashov, 1984) which points toward the existence of a highly refined ability to differentiate between potential hosts.

The reason for fleas remaining in the host's nest is simply because their food is located there. Adults feed directly upon the host's blood, while the larvae feed upon the fecal material produced by the adult fleas. Sharif (1937) has reported that dried blood and yeast was used in laboratory tests and obtained almost 100% success in rearing fleas from larvae to adults. Eleven years later he reported that blood alone was unsuccessful in bringing about pupation and cocoon formation for three species of *Xenopsylla* (Sharif, 1948). The addition of yeast to the blood meal resulted in normal growth. Additionally, Sharif reported that flea larval food deficient in B vitamins was inadequate for proper development and that B-vitamin producing microorganisms need to be associated with the food in order for successful development to occur (Sharif, 1948). A scavenging role has been reported for at least one species by world-renown flea researcher Miriam Rothschild when she stated that larvae of *Spilopsyllus cuniculi* burrow into the hair and feed upon the tissues of baby rabbits who have recently died in the nest (Rothschild, 1975). Generally speaking, it is now widely held that fleas feed on a variety of organic matter in the environment.

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[2] Personal conversation dated January 23, 1995.

These studies point out the dependence of fleas upon blood, as well as their dependence upon other "organic materials" in the environment. Flea larvae will likely need a blood meal at some point in their life cycle, yet they can survive adequately for some time on alternate food sources if blood is not available. This means a flea egg that hatches relatively far from the host, will be able to feed and grow for some time until a blood meal can be procured. It would behoove the flea to possess some system for locating the host if it is dropped off (in the egg stage) relatively close to the nest, since the chance of locating a blood meal is inversely proportional to the distance from the nest.

As important diet for rat-flea larvae in nature consists of both rat and flea feces. Different species of rat flea, and presumably all fleas, can survive on poor diets more successfully than related species (Sharif, 1948). In a domestic rat burrow, diverse organic matter may be found, it varies in diverse localities, and may be influenced by prevailing weather conditions in an area (Sharif, 1948). For these reasons, one may find only some species of flea in one area, while another species may be far more successful in a different area. The distribution of various flea species would then be somewhat governed by the ability of the flea to survive under poor nutrient conditions. Indeed, it may have little to do with the appropriate host for the flea, and more to do with the quality of the food source which dictates what flea will infest a particular host.

Fleas may attack a wide variety of hosts, however, they preferentially do so on only one or a few hosts. One study of 667 Egyptian dogs found 9,008 specimens of the cat flea, *Ctenocephalides felis*; 1,090 of the human flea, *Pulex irritans*, 349 of the dog flea, *Ctenocephalides canis*; 29 of the sticktight flea, *E. gallinacea*, and 6 of a rat flea, *Xenopsylla cheopis* (Amin, 1966). The 29 specimens of *E. gallinacea* were all found on one dog who roamed alongside chickens, however, it is apparent that the predominant flea by far is the cat flea, followed modestly by the human flea. The high incidence of the human flea on dogs probably had something to do, similar to *E. gallinacea*, with the close proximity the dogs had to humans.

This host specificity has led to the characterization of various host features. For example, I have already mentioned that the hairs or spines of the flea larvae can be found on free-living species. *Uropsylla tasmanica* has no spines except for its first instar, and *Echidnophaga gallinacea* has only reduced spines. Neither of these can be considered free-living species since the first is an endoparasite, and the second cannot successfully parasitize free-living hosts, but only those hosts (chickens) who are restricted, or penned in chicken coops. If the spines are functioning as electromagnetic antennae and if they are used for locating a host, where their food source is falling off of, then one might anticipate a non-feeding flea larva to be lacking in spines. This is exactly what I found when I stumbled across an article by Barnes and Radovsky (1969) describing at the time, a new species, *Tunga monositus*, that does not feed in its immature stages. As I expected, one of the distinctive characteristics separating it from virtually all other species is its reduced setation. The possibility that a flea could "phase out" an unnecessary organ finds support in this very species. Rudimentary mandibles are present on the flea larva which apparently are a remnant from a time when they did feed. The phasing out of both mandibles and spines may be following the same course.

Is the presence of spines on flea larvae related to their free-living existence? Since *U. tasmanica* is no longer free-living, is this why it is losing its spines? Do the reduced spines of *E. gallinacea* in turn reduce its fitness when compared with other chicken fleas who are more successful at parasitizing and reproducing with free-roaming chickens? Is *Tunga monositus* phasing out its own spines because they are no longer needed for host location? All flea larvae that I am aware of that need to find their host possess long body spines. Conversely, I have only been able to locate in the literature three species of flea larvae who have no need or apparent ability to locate a host, and all three have reduced setation.

A brilliant and comparative study by Traub (1968, 1969, 1972) and colleagues (Traub and Barrera, 1966; Traub and Dunnett, 1973; Traub and Evans, 1967) of the spines and combs of adults of a large number of species has demonstrated their adaptive modifications which are often related to the affinities and habits of their host. If the arrangements and types of spines are related to the lifestyles of adult fleas, is it not possible that the arrangements and types of spines of the larvae may reveal a similar relationship as well?

The Cat Flea

The cat flea, *Ctenocephalides felis*, is an important urban, medical, and veterinary pest year-round in Florida and in indoor climates of the North. Under favorable weather conditions, they can reach large numbers outdoors as well. The cat flea has taken well to living indoors and because of this has developed an unpopular reputation among many homeowners who have a cat or a dog. Despite the given name "cat flea", they are the most common flea on both cats and dogs (Ebeling, 1975). Their specific name, *felis*, of course refers to the cat's generic name (*Felis catus*) while the cat flea's generic name, *Ctenocephalides*, means literally "comb head" thus referring to the distinctive comb-like structure behind the adult's head (Fig. 3-1). They have been the subject of extensive research in an all out effort to manage their numbers. Not only are their bites annoying to both pets and their owners, but cat fleas are the intermediate host of dog tapeworm, *Dipylidium caninum* (Chen, 1934).

This research work also seeks population management of the cat flea. Ultimately, some control over cat fleas especially in the urban environment would be highly desirable by this researcher. However, I will not take the usual insecticidal/toxicological route, but instead will focus on understanding the cat flea's behavior a little bit better than when I first began researching this fascinating insect back in 1994.

Basic information on internal and external morphology of the cat flea is surprisingly lacking. Accounts were given by Laboulbene in 1872, by Kunckel in 1873,

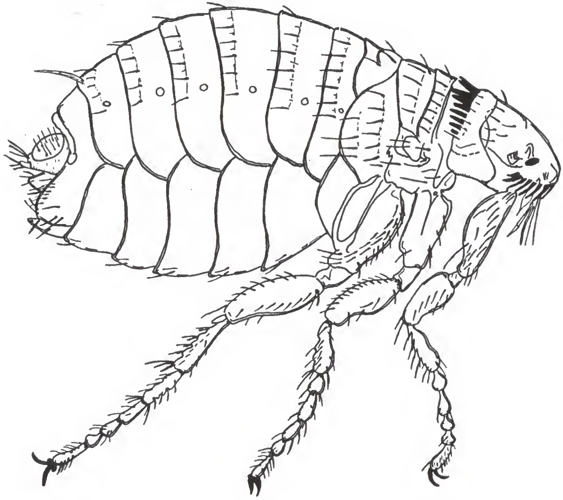

Figure 3-1. The adult cat flea, *Ctenocephalides felis*, Siphonaptera: Pulicidae.

and Patton and Craig in 1913, none of which, however, I have been able to obtain. A more recent account was given by Kir'yakova in 1961, but this was in Russian.

The life cycle of the cat flea is rapid under ideal conditions. At 24°C, they may reach adulthood in 20-24 days (Harwood and James, 1979). The larval stage may only take 11 days. Cat flea larvae remain in sandy soil outdoors, but kitty litter is a welcome medium in urban environments. They will burrow just a few millimeters under the surface (Kern, 1991) perhaps as an escape response to predators such as ants. Cat flea larvae are unable to move rapidly in sand, so when they wish to do so, they briefly emerge to scurry across the surface, only to burrow again shortly thereafter (Kern, 1991).

On average, the female cat flea can lay one egg every hour, or 24 per day (Hinkle et al., 1991). A female flea can produce over 150 eggs in her lifetime (Osbrink and Rust, 1984), and the average production on a cat containing over 200 fleas will exceed 5,000 eggs (Kern et al., 1992). The adult's average lifespan on the cat was calculated by Osbrink and Rust (1984) to be only nine days.

The larvae upon hatching are immediately mobile and search for food. Larvae may migrate several meters in 24 hours (Kern, 1993) and a mere 47-50% of the flea larvae were located where the cat spent 90% of its time (Kern, 1993) thus indicating there are potential, but unknown factors regulating larval migration.

The larvae will consume feces excreted from the adult fleas who may consume over 15 times their own body weight in blood per day (Dryden and Gaafar, 1991). This nutritious source coming out of the "back end" of the flea will consist of unhydrolyzed blood, as well as some partially digested blood (Hinkle et al., 1991). Cat flea larvae were unable to complete development without feeding on adult flea feces or dried blood (Moser, 1989). Dried bovine blood is a good blood source that successfully develops fleas into adulthood under laboratory conditions (Moser et al., 1991).

Cat flea larvae may be different than most other fleas in this respect. Strenger (1973) found that they were unable to develop on a variety of substances naturally available in their environment, such as decaying vegetable matter, feathers, and cat feces. Additionally, he reported that the larvae may survive on cat flea eggs after the first molt. Since adult cat flea feces and eggs are both dropping from the host, and they are so necessary for cat flea larval development, then locating the host should be of prime importance for the larvae. In fact, it would be a matter of life and death.

CHAPTER 4
MATERIALS AND METHODS

Flea Colony

Cat flea larvae were obtained from a laboratory colony maintained at the U.S.D.A. Medical and Veterinary Research Laboratory in Gainesville, Florida. The flea *in vivo* rearing method was described by Hinkle et al., 1992. Larvae were sifted from a sand medium with a U.S.A. Standard Testing Sieve No. 18, 1 mm opening size. Only second and third instar larvae could be sieved because early second instar and first instar larvae easily passed through the grating. Sexing is not possible for flea larvae, therefore, both sexes were used in this study.

Late third instar larvae purge their guts and are easily identified by their white color. Profound changes occur in holometabolous larvae just before pupation as Loeb and Dodson (1984) discovered when studying the moth, *Heliothis virescens*, which showed progressive changes in stainable neurosecretion of the brain. This is known as the wandering stage in flea larvae when, like many holometabolous larvae, they seek out a suitable pupation site. Since behavior of the flea larvae changes drastically during this period, the presence of even a few of these larvae in a batch of thousands disqualified the entire group from experimentation since gut purging is already the final phase of the wandering stage. Therefore, the age of cat flea larvae used in this study fell between a narrow “window” of from late second to early third instar. Cat flea larvae developed and matured through this time period in approximately two days.

During this study, most of the larvae were received in a small plastic vial along with some of the white hobby sand they were reared in at the U.S.D.A. laboratory, (EPK sand, C.A.S. No. 14808-60-7, Feldspar Corporation, Edgar, Fla.) and a little food (dried bovine blood) sprinkled on top. These larvae were maintained as received in a semi-enclosed plastic container in order to conserve humidity. The larvae were removed from the vial for experiments, and individually separated with a softened painter’s brush. Softening the brush was achieved by cutting off most of the bristles, thus allowing the remaining bristles to bend more freely.

At the conclusion of the experiments, the fleas were placed back in the vial for use the next night. Fresh larvae were received from the U.S.D.A. laboratory three times per week, thus insuring a ready supply of flea larvae of the correct age. No adults were used in any experiment of this research, therefore, larvae were routinely killed before pupation by freezing. Occasionally however, some larvae were allowed to pupate into adults. This was only done in order to test their vigor and insure the adequacy of the rearing conditions away from the laboratory. All fleas allowed to pupate and emerge, produced normal, apparently healthy adults.

Experimental Conditions

Several different rooms were used for this study. The first was a small office space in the U.S.D.A. Medical and Veterinary Research Laboratory, which was windowless and approximately 2.5 m by 2.5 m. Both the temperature, 22°C, and humidity, 55%, were tightly regulated in the building. All pilot experiments were performed in this office.

The majority of the research, however, took place in a large biophotonics laboratory measuring 8.23 m x 4.57 m, and with a 2.74 m x 0.86 m window, even though the curtains were drawn during all experiments. Relative humidity and temperature conditions were not as tightly controlled but allowed to vary with Florida's naturally high humidities. These conditions allow for a more natural range to which a Florida flea might be exposed. The mean temperature was 26° C (+/- 3°) while relative humidity readings averaged 86% (+/- 8%).

A light reading of only 3 foot candles, as determined by a General Electric Foot Candle Meter, was measured at the center of the laboratory. The center was the precise location of all experiments[1]. Interference from 60 Hz frequencies and strong, artificial electromagnetic fields emanating from the walls were greatly reduced by running all experiments in the center of this laboratory. Electromagnetic (EM) fields emanating from the walls, due to the presence of electrical wiring, fell off to baseline levels at from 0.5 m to 1.2 m depending upon plugged-in electrical devices in the immediate vicinity. The corners of the room showed even greater field intensities such that a distance of 1.5 m from each of the two walls forming a corner was required before the EM fields were reduced to baseline levels. All experiments were run at the center of this room which meant distances of from 2 to 4 meters were maintained from any one wall. At this location, the electromagnetic field was relatively steady at 0.013 V/m, with no artificial fluctuations originating from the immediate surroundings. All electromagnetic fields were measured with a Radio Shack® Digital Multimeter set to measure alternating currents (AC) on a 200 mV scale (chosen to reduce flutter). The antenna used was a Photonic Ionic Cloth Radio Amplifier antenna, or P.I.C.R.A.M. (Callahan and Kornberg, 1993, Patent No. 5,247,933).

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[1] For comparison, the same instrument measured 70 foot candles outdoors on a cloudy day.

No extraneous sounds were present in this room, either from an air conditioner or similar electronic device as measured by a Realistic® Sound Level Meter. The research room was measured at less than 0.5 decibels which was the instrument's limit[2].

Virtually all of the experiments tested a behavioral response of the flea larvae to a human stimulus. In all cases, I was that stimulus. My presence in the experiments was also necessary to record the relative movements of the flea larvae in the petri dish and to observe any behavioral trends that occurred during the experiments.

For many of the experiments, two simultaneous experimental positions were used. The first was on my right and the second was to my left. In this way, the behavioral response could be verified, unquestionably as orienting to me and not anything in the research room, and also served to double the number of repetitions during a particular night's work. No noticeable differences were observed between the behavioral responses of the flea larvae on my right and on my left sides. Almost all of the experiments were conducted at night in order to ensure no other human presence in the room. A few of the experiments were conducted during the day, only when it was verified I would remain undisturbed, as well as to insure that the behavioral response was not relegated only to nighttime hours.

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[2] For comparison, a reading of 60 decibels was recorded approximately one meter from a flushing toilet.

Data acquisition

Flea larvae were placed in plastic petri dishes, 15 cm in diameter (Thomas Scientific) which in turn were placed on top of a paper grid, thus dividing the area of the petri dish into nine equal sections of 40° (Figure 4-1). The center region, where these nine regions normally converged to a point, was arbitrarily designated "Section 0". This "Section 0" was devised because if flea larvae were located at the center of the dish, they could crawl and/or stretch across several sections. The number of times larvae were found in Section 0 was at or below 1.00% for all experiments run. Therefore, because of the low percentage, these data points were considered as "lost data" and not tabulated with the final statistics.

If groups of larvae (50 or more) were used in a particular experiment, then only the final location of the larvae at the conclusion of one hour, and which remained in a

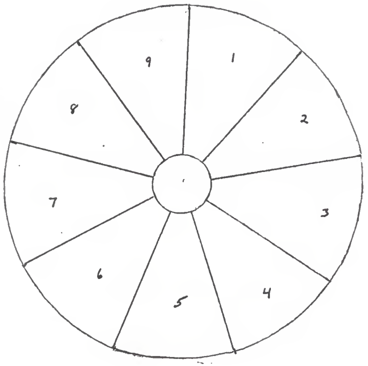

Figure 4-1. Grid used for dividing the petri dish into nine equal sections of 40°.

close-knit aggregation, was recorded. The height experiments, the electromagnetic field experiment, and all pilot experiments were conducted under these circumstances. These results have far fewer data points than the remaining experiments listed below (28 or less vs. 900 or more), but are far more precise because they are a measure of the final decision of the group, and do not take into account random movement before final orientation occurred. As the experiments progressed, a reduction in the number of flea larvae available necessitated a slightly different form of data acquisition using less than 50 larvae per petri dish.

When from one to ten larvae were used in an experiment, the location of each larva was recorded every two minutes for the duration of the hour-long experiment. It was observed in pilot experiments that most flea larvae could orient to me in approximately 20 minutes, and that if no orientation occurred after one hour, no orientation was likely to occur. Therefore, all experiments were run for one hour in order to standardize response time. Data acquisition in this manner was not as precise when less than 50 larvae were tested in a petri dish, however, this did allow for a breakdown of individual flea larval movement throughout the course of that hour. Time increments were arbitrarily chosen for analysis in order to determine how quickly an orientation response occurred, as well as to determine the dynamics of this response over the course of one hour. Increments of 10, 20, and 30 minutes were chosen for analysis. Graphs and statistical analysis of this breakdown data appear in Chapter 6 as well as the Appendix while a graphical summary can be found in the Results section (Chapter 6)

Height experiments

A ten-level structure was constructed in order to test the flea larvae at various heights above the ground and in relation to the human stimulus. The levels began at ground level and continued upward for ten additional levels separated by 15 to 20 cm increments. The first level was at 0.29 m, Level 2= 0.48 m, Level 3= 0.66 m, Level 4= 0.86 m, Level 5= 1.06 m (head level for human while sitting in a chair), Level 6= 1.33 m, Level 7= 1.52 m, Level 8= 1.71 m, Level 9= 1.89 m, and Level 10= 2.11 m. The skeleton structure was made completely from wood, including the dowels used to support the shelves. The shelves however, were constructed from polystyrene sheets cut to size and wrapped in plastic wrap so as to prevent flaking. Neither ferromagnetic nor essentially paramagnetic materials were used. This structure was not comprised of any flattened wooden boards, but consisted of a skeleton structure designed specifically to allow for free air movement. The shelf dimensions were 61 cm x 37.5 cm x 1.9 cm. The four legs of this shelving unit were placed into buckets of sand 12.7 cm deep in order to reduce the propagation of floor vibrations stemming from human movement in the laboratory as well as structural perturbations. Based upon the results of the height experiments, all remaining experiments were run at a height of between 76-81 cm above the ground (about table level).

Electromagnetic field experiments

The presence or absence of an alternating (60 Hz) electromagnetic field was the modifying variable during the particular experimental runs testing the response of a group of flea larvae and their response to an EM field. The artificial field was created by simply plugging in three electronic devices into an electrical outlet, thus creating an alternating electromagnetic field emanating from the individual devices. These electrical devices included a General Electric® AM/FM stereo radio and cassette recorder, running on 120 volts with an input of 10 watts; a Sharp® Microwave Oven, running on 120 volts with an input of 600 W and a frequency of 2450 MHZ; and a Black & Decker® Spacemaker Oven (no specifications available). All three electrical devices were simultaneously plugged in to wall outlets, and therefore emanated an electromagnetic field modulated by a 60 Hz frequency (U.S. Standard) at 4.1×10^{-3} V/m at a distance of about 2 meters (the location of the petri dish containing the flea larvae).

Magnet experiments

The magnets used in this study included only two types. The first type included some small disk magnets that measured 1.9 cm in diameter and 4 mm in thickness, and whose magnetic field measured between 550 to 720 Gauss, depending upon the magnet. Combinations of these small magnets (one on top of the other) caused slight increases in the magnetic field to occur with values reaching 760 or even 800 Gauss. No increases in magnetic fields should have occurred if the magnets were all perfectly equivalent and with the North and South poles perfectly aligned. Because the magnets were not perfect, slight variances in magnetic field intensities resulted when they were placed together. Only two of these magnets were placed together for a series of experiments as designated in Chapter 6.

The second type of magnet was a large horseshoe magnet (10 x 9 x 8 cm) that measured between 1950 and 2500 Gauss depending upon the precise location of the probe. Magnetic field measurements were performed with a Bell 610 Gaussmeter.

All petri dishes containing the flea larvae were touching the magnets throughout all experiments involving a magnet. The location of the magnets was judged solely by its relative position to the human stimulus, where 0° was designated directly away from me, and 180° between me and the petri dish. The designations 90° and 270° refer to my right and left sides, respectively, and were situated midway between 0° and 180°.

Two other locations of the small magnets were also utilized for several experiments of this study. The first location was directly on top of the petri dish at its midpoint. These experiments are labeled in this dissertation as "top/center". The other location was directly opposite but beneath the petri dish. Unfortunately, one magnet was not wholly reliable at balancing the petri dish. Therefore, four magnets were placed under the petri dish simply for stability. These four magnets were directly adjacent to one another and formed a square configuration under the centralized portion of the petri dish..

Fan experiments

The fan used in designated experiments was a Radio Shack cooling fan, running on a 60 Hz plug and using 12 W. Air speed was determined to be 5.05 m/sec, as measured by an Official Weather Bureau Field Model (Davis Instrument, Baltimore, MD). A rectangular, flattened wind tunnel was constructed with wooden sides and a glass top. The dimensions of this tunnel were 48.3 cm x 34.3 cm x 1.6 cm.

Competing human stimuli

Another individual was brought in to the experiment in order to test the response of the flea larvae to me while another human was present. The other individual situated himself the same distance away from the petri dishes containing the flea larvae, with both of our "right sides" to the fleas. Positions were switched midway through the experiments. The other individual was approximately 6.8 kg (15 lbs.) heavier than me and chosen to give the fleas a choice between two slightly different body types. I leaned over the petri dishes throughout most of the experiments in order to record the fleas' positions. The other individual was asked to lean over the fleas during the last eight minutes of one run, in order to test the fleas' reaction. Ten flea larvae were placed in a single petri dish for all runs.

Statistical analysis

All data points were transformed into frequency distributions for nine sections and plotted on radar graphs, thereby representing the percentage of time the fleas were found within a particular section. These percentages, or frequency distributions, were used to calculate goodness of fit to a circle. A chi-square test comparing the frequency distributions of the nine sections was compared with an expected value of 0.11, which is the expected value of all nine frequencies if random movement occurred. The radar graph depicting random movement would simply be a circle. The degrees of freedom for the chi-square test was 8 (9 sections - 1) and the p value was conventionally chosen to be 0.05.

Testing the goodness of fit to a circle did not allow me to determine whether one graph was more directive toward section 5, where I was always positioned, compared to another graph. When examining all the graphs it was observed that movement outside of sections 3, 4, 5, 6, and 7 was predominantly random and largely irrelevant. I was most interested in that part of the graph on my side of the petri dish, namely those five sections just mentioned. Further examination revealed that the most highly directive responses showed significant differences within only three sections, those being sections 4, 5, and 6. For this reason, a statistical analysis utilizing the chi-square test was initiated that only focused upon these critical sections.

The degree of directivity (D.O.D.) for an experiment was calculated using a variant of the same chi-square test used for determining the goodness of fit to a circle.

One difference between the chi-square test and the D.O.D. test was that all sections were used in the former while only three to five sections were used to calculate the latter. If three sections were used to calculate my analysis, they were sections 4, 5, and 6, while sections 3, 4, 5, 6, and 7 were used when calculating five sections. A goodness of fit to the mean of the three or five frequency distributions was chosen as the comparative value.

The chi-square values obtained from this analysis were combined in order to obtain a composite chi-square value. Because a highly directive response was reliably indicated with as few as 3 sections, the emphasis was placed upon the chi-square value obtained from the three sections over that value obtained from the five. For the sake of simplicity, the composite value was computed by doubling the chi-square value obtained with the three sections and then adding the chi-square value obtained from the five sections, thus placing a larger emphasis on the three section response. This composite chi-square value is the number designation for degree of directivity, or D.O.D., used in this dissertation. This final D.O.D. value, was not relatively compared to a predetermined statistical p value. Instead, the absolute D.O.D. value was directly compared with other D.O.D. values obtained from the remaining experiments. In this way, a linear “index” of which graphs were more directive than others, and hence which experiments produced more directional responses, was obtained.

External morphology

Sensilla lengths were measured from a minimum of twenty sensilla, taken from at least six individuals. The images from a dissecting microscope were relayed to a Kontron IBAS-AT video image analysis system and measurements were made using a calibrated digitizing tablet.

General morphological features of the cat flea larva were made with a standard Nikon stereomicroscope under the highest magnification and fiberoptic lighting to prevent drying out of the specimens. Dozens of larvae were examined to arrive at a composite picture representing a generalized cat flea larva (see Chapter 6).

CHAPTER 5
THE PILOT EXPERIMENTS

Introduction

While observing flea larvae in the laboratory back in 1994, a curious behavior was accidentally discovered. One hundred flea larvae or so were placed in a petri dish and then positioned beside me. Regardless of the location of the petri dishes surrounding me, the larvae always aggregated on the side of the petri dish facing me. This was repeated dozens of times, and I was intrigued enough to turn this discovery into a dissertation study.

Because this apparent attraction the fleas displayed toward a human stimulus has never been published and I am apparently the first to document such a behavior, a wide variety of pilot experiments were designed in order to characterize the behavior, and to determine what limitations this behavior exhibited. What follows is a brief summary of the pilot experiments conducted that subsequently laid the foundation for the dissertation research. The experiments are listed roughly in the order in which they were conducted.

The Experiments

Experiment 1

Flea larvae were placed into a petri dish and shaken gently so as to evenly disperse the group. The flea larvae were observed to form groups, or aggregations, within the first couple minutes. Following this, the aggregation, not the individuals necessarily, would move from their preliminary position and orient to me in about 10-30 minutes. Most importantly, they never moved from this final position. This reaction was a "positive orientational response" and was the standard whereby all subsequent experiments were compared.

Experiment 2

Cat flea larvae undergo three instars, or developmental stages, during their larval life. During the time period immediately preceding pupation, many insects exhibit wanderlust and spend their time searching for a suitable place to pupate. Flea larvae also exhibit this behavior called "wandering behavior" and showed no orientational response to a human stimulus during this period.

Experiment 3

Flea larvae in the late third instar stage were collected together toward one end of the petri dish, or sifted to the center of the petri dish so as to form an "unnatural" aggregation. None of these aggregations were stable, and all flea larvae evenly dispersed themselves within just a few minutes. It was determined that all experiments testing the orientation response must occur with larvae before they reach this critical stage in their development.

Experiment 4

Books, magazines, or newspapers were placed over half of the petri dish in order to create a shadow effect on one half of the petri dish. No matter the location of the shadow, all larvae moved to my side of the petri dish (a positive orientation response). If the cat flea larva was negatively phototactic, as has been anecdotally mentioned in the literature, then attraction toward a human stimulus was stronger.

Experiment 5

Considering that there could be shadows or horizontal movement that the larvae might be attracted to, their petri dishes were placed in a white enamel coated (metal) pan that was itself 5 cm deep. The white sides of the pan would prevent the horizontal detection of visible light caused by me, but would not exclude detection of visible radiation through the top of the petri dish. Only positive orientational responses occurred under these conditions.

Experiment 6

To exclude all visible light from the flea larvae, they were next placed in one of two cardboard boxes[1] with tops. When the boxes were opened up 37 minutes later, all flea larvae were found to have exhibited the same positive orientational response, and with apparently the same intensity. Even though flea larvae do not possess eyes, it was felt at the conclusion of these initial experiments that electromagnetic radiation in the visible spectrum was probably not involved in this orientational response.

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[1] One cardboard box measured 5.7 x 33 x 24.8 cm and the second measured 27.3 x 32.4 x 35.6 cm.

Experiment 7

Flea larvae were allowed to complete their orientational response, and then the petri dishes were carefully rotated 180°, such that the larvae were now directly opposite my location. At first, the larvae were apparently unwilling to break up the established aggregation. All experiments eventually displayed a fascinating reaction whereby the larvae slowly crawled to the side of the petri dish toward me, but the response time was often much longer than 10-30 minutes.

Experiment 8

Flea larvae were allowed to complete their orientation response as before. The petri dish was gently shaken to disperse the group; however, the aggregation began to form on my side of the petri dish within 2-6 minutes. Repeat runs using the same larvae were found to show greatly reduced times over the primary run. It seemed that once the larvae had "tuned in" to a human stimulus, they could locate the human source much quicker. (Compare to the response of flea larvae to two human stimuli in Chapter 6.)

Experiment 9

Flea larvae were placed at varying horizontal distances from me in order to determine the range of the orientation response. All experiments revealed a positive orientational response for all distances up to 2 m (the maximum distance tested).

Experiment 10

Continuing upon the theme of Experiment 7, petri dishes containing larvae were placed at varying locations about me in the office, and all experiments where the petri dishes were placed above my head level, while I sat in a chair, showed no orientational response.

Experiment 11

A third variation upon the theme of the last two experiments was to place the petri dishes containing larvae upon the floor, again while I remained in a chair. Relatively slow orientation responses occurred in 1.5 to 2 hours.

Experiment 12

Petri dishes containing flea larvae were placed in various closed drawers of a metal desk that I was seated up against. Random responses were observed.

Experiment 13

This experiment was conducted in the dark with three petri dishes containing larvae. Unlike Experiment 6 of this chapter, both the stimulus and the fleas were in total darkness. No orientational response was observed after almost two hours of waiting. As soon as the lights were turned on, the three groups began to move in my direction, within just a few minutes, and completed their orientation response in from 30-55 minutes.

Experiment 14

Petri dishes containing larvae surrounded a few small pieces (about pebble size) of dry ice. No orientational response occurred at varying distances of 15-30 cm from the ice.

Experiment 15

Flea larvae were placed in petri dishes and situated at various heights above the ground. I stood up and placed my body approximately 10-15 cm from the petri dishes. No orientation occurred from the larvae in the petri dish that I continually "breathed" upon for 45 minutes. An orientation response did occur from the flea larvae placed at the level of my waist.

Experiment 16

A group of larvae were given a choice between burying themselves in clean sand (with no food) and a small pile of food. Each of these piles were placed opposite the other while the flea larvae were introduced at the center of the petri dish. All larvae buried themselves in the sand and remained so for hours.

Experiment 17

Flea larvae were placed either in a clean petri dish, or one containing a thin layer of sand. The larvae that remained exposed moved rapidly and never stopped moving. The larvae with even a thin layer of sand would eventually settle down and remain motionless for over an hour. It seemed obvious that the flea's preference to bury oneself is a powerful behavioral response. A decision was made that in order to test the response of larvae to various stimuli, a clean petri dish would be necessary so that "burying behavior" would not interfere with their other responses.

Experiment 18

Flea larvae were allowed to form their aggregations and then closely observed for up to 2 hours. The dynamics of an aggregation when it first forms, as observed through a dissecting microscope, is such that the larvae on top are continually "drilling" down into the clump of larvae beneath them. This behavior is intense for the first 20 minutes or so, but eventually slows down. After one hour, the larvae were virtually motionless in this aggregation and remained so for an additional hour unless they were disturbed.

Experiment 19

Anecdotal information has suggested that fleas are negatively phototactic. It was possible that the flea larvae were forming aggregations as a means of burying themselves in an attempt to escape from the light. Therefore, an experiment was conducted whereby the flea larvae were placed into a petri dish and gently shaken as before; however, they were then placed into cardboard boxes or the lights were turned out in the room. In all cases, the fleas were found to have formed perfect aggregations under both conditions. Apparently, the aggregation response was light-independent.

Experiment 20

Flea larvae were placed on their rearing sand with the lights out. When the lights were turned on five minutes later, all larvae were found to have already buried themselves. Similar to the above experiment, burrowing behavior also appeared to be light-independent.

Experiment 21

Flea larvae were allowed to form the positive orientation response to me while the petri dish was placed under a dissecting microscope viewer. After the response was established, the fiberoptic lights were twisted around to shine directly upon them from my direction. All flea larvae remained oriented in my direction and made no attempt to move away from the intense light source.

Experiment 22

Larvae will not crawl against a wind source, even if the wind speed is barely perceptible to humans (tested by using a wet finger). Apparently, they are not as likely to follow a scent upwind as many moths are reported to do. It seems likely, based upon the frail nature of the flea larvae, that they are more prone to desiccation, so this factor may be involved in this observed response.

Experiment 23

A 4-watt light bulb was wrapped in black electrical tape and used as an infrared source. Flea larvae showed an initial attraction to the point source in as little as 10 minutes. Not a single aggregation that initially formed near the bulb remained so at the conclusion of the designated hour. In fact, many of the fleas were found directly opposite the source at the completion of the one hour experiment. This response was not always repeatable, variable responses were noted but did not appear to be random. Often the response was either toward or away from the infrared point source. Varying distances of from 1 cm up to 15 cm were tested but, once again, the results were not easily discernible, even though it was obvious that a response to the heat was occurring.

Experiment 24

A black cardboard piece was placed between the bulb (described in the former experiment) and the fleas. The stimulus heated up the black cardboard and emitted a much broader infrared stimulus than the "point source" of the former experiment. The results were the same.

Experiment 25

Convected or radiant heat was the possible stimulus for the previous experiments and so a fan was set-up in order to create a laminar flow of air between the bulb and the black cardboard sheet, thus disrupting convective heat from reaching the black cardboard but allowing pure infrared wavelengths to strike the sheet, where they would eventually transmit. The immediate orientation to the bulb so evident in the former experiments was no longer observed, showing that convective heat may indeed have been the reason for the initial attraction.

Experiment 26

House fly larvae, *Musca domestica*, younger than the wandering stage were tested in the same petri dishes and under the same conditions as the flea larvae. No orientational response was observed, for even a minute, over the course of two hours.

Conlusions

1. All experiments should be conducted for one hour. This would allow the fleas to form an orientational response.
2. This orientation response was strong and might take precedence over alternate behaviors.
3. Second and early third instar larvae should only be used for all experiments.
4. Visible light was probably not mediating this response.

5. All experiments should be conducted within two meters of a human stimulus.

6 The height at which they were positioned above the ground and/or in relation to me was important in their ability to form a positive orientational response.

7. The orientational response may be mediated somehow by electromagnetic energy.

8. Carbon dioxide did not appear to be an important factor.

9. All experiments should be conducted in perfectly clean petri dishes.

10. Thermal heat influenced the flea larvae, but it was not established whether this mediated, in any way, the orientational response toward me.

11. The observed response may be specific to flea larvae.

CHAPTER 6
RESULTS

Miscellaneous Experiments

Second instar cat flea larvae begin to form aggregations in as little as 30 seconds. The mean time to complete one of these aggregations was calculated to be 6.20 minutes (SD= 3.25, n= 65). This value is somewhat arbitrary since it was difficult to tell exactly when the fleas were "finished" aggregating. However, it will serve to give the reader some idea of how quickly they do form.

Cat flea larvae immediately begin to bury themselves in sand the moment they are placed upon it. Mean time to submerge themselves in sand, as measured by a stopwatch, was 33.1 sec. (SD= 23.6, n= 38). Final times ranged from 7.5 sec. up to 2:03.2 min.

Height Experiments

The results from the height experiments are graphically displayed in Figure 6-1. Results show that the ability of the fleas to orient to a human stimulus is excellent up to about 1.1 m (Level 5), which is at head level when I am seated. At slightly higher levels (6 and 7) the flea larvae are not as accurate in locating the human stimulus, while at levels

8, 9 and 10 apparent disorientation is observed. A curious bipolar orientation occurred for these top three levels.

Chi-square analysis for goodness of fit to a circle (i.e. random movement) revealed that all of the results were not significantly random (Table 6-1). Large chi-square values for heights 2 through 5 suggest large differences between the remaining levels tested. These heights showed the largest deviations from a circle and were considered the best results. Further analysis utilizing degree of directivity (D.O.D.) index values (Table 6-1) also show that heights 2 through 5 display a highly directive tendency toward Section 5, the location of the human stimulus, and therefore the section to which the D.O.D. index was compared. The D.O.D. index falls off significantly above height 5.

Number Experiments

Results testing the response of a specified number of larvae in the petri dish to me are graphically displayed in Figure 6-2. The graphs all show the ability of one larvae, two larvae, five larvae, and ten larvae to orient to a human stimulus located at Section 5. The ability of the larvae to orient appears to improve with increasing number of larvae in the petri dish. This finding is visually apparent as an increasingly "pointed" graph directed toward Section 5. This improvement in directivity is supported by the D.O.D. index (Table 6-2) which shows steady improvement in directivity of the graphs toward Section 5 as the number of larvae in the petri dish increases from one to ten. This improvement was predicted since the D.O.D. index greatly increases when 50 or more larvae are used (Table 6-1).

Chi-square analysis (Table 6-2) for goodness of fit to a circle ($x^2 = 15.5$, $p= 0.05$, $df= 8$) revealed three of the four graphs to be significantly different from a circle. The only graph not significantly different from a circle is the "5 larvae" graph. Its chi-square value was 12.48. The other three graphs all had chi-square values exceeding 15.5 (Table 6-2) which means three of the four experiments show random movement *not* to be occurring. This suggests that there is a directive response as shown by these remaining graphs, but the test does not tell me in which direction. For this determination, visual analysis of the graph is conducted in order to determine what direction the graph is pointing in. Most of the graphs point toward Section 5, therefore, this was the section to which the degree of directivity (D.O.D.) test was compared.

Magnetic Experiments

Results from experiments involving one small magnet, two small magnets, and one large magnet all showed an interesting trend. All three experiments showed significantly random behavior when the magnet was placed between the petri dish and the human stimulus (180°). Chi-square values decreased from the one to two magnet experiments and then to the large magnet experiment which suggests that random behavior becomes more pronounced with increasing field strengths.

A similar effect was observed when the small magnet was placed on top of the petri dish. Not only did random movement result (Table 6-3) but their ability to locate me and thus orient was inhibited even more so (D.O.D. index of 2.42) than when magnets were placed at 180°. Due to the weight of the large magnet and the low visibility of the petri dish from the researcher's viewpoint, the experiment with the large magnet placed at the top/center of the petri dish was not conducted.

Figures 6-3, 6-4, and 6-5 depict the relative movement of the flea larvae when exposed to one magnet, two magnets, or the large magnet, respectively. The graphs shown in Figure 6-3 display results that were largely expected. However, after close examination, Figures 6-4 and 6-5 reveal some rather interesting and unexpected results. In Figure 6-4, flea larvae were found to spend noticeable periods of time around Sections 8, 9, and 1. This effect was observed in various degrees for all the graphs in Figure 6-4.

Figure 6-5 shows random movement of the flea larvae when the magnet is placed at 180° but the other three graphs show the flea larvae to be spending more time in the sections directly adjacent to the large magnet. When the large magnet is placed at 0°, the graph curiously points toward Section 1, which is a measure of where the larvae spend more of their time. When the large magnet is placed at 90° the flea larvae spend more time in Sections 2 and 3. Lastly, when the large magnet is placed at 270°, the fleas can be seen once again to spend more time on that side of the petri dish where the magnet is located, namely Sections 6, 7, 8, and 9 over the time that they spent in Sections 1, 2, 3, and 4.

Magnet 10 Experiments

Four previous experiments in particular showed a striking randomness not found in the other experiments. The first three are the experiments whereby magnets were placed at 180° and the second was the experiment where a single magnet was placed on the top of the petri dish. Increasing the number of larvae in the petri dish increases the D.O.D. index, as was shown in the Number Experiments, and so these four experiments with the magnets were repeated, but this time with 10 larvae in order to determine if the fleas could overcome the effects of the magnetic field and orient to me as such.

The presence of 10 larvae in the petri dish did noticeably affect two of the four experiments (Figure 6-6). The two experiments affected included the single magnet at 180° as well as the single magnet on the top of the petri dish. These experiments did not show random movement (Table 6-4) as they did when only one larva was in the petri dish (Table 6-2). The graphs show an extremely directed response toward Section 5 (Figure 6-6) and the D.O.D. indices of 63.22 and 67.85, help to support this very obvious conclusion (Table 6-4). These D.O.D. indices even exceed that of the control (D.O.D. index of 50.18) for 10 larvae in a petri dish as obtained from the Number Experiments (Table 6-2).

The remaining two experiments that still showed statistically significant random movement of the fleas included the two stacked magnets and the large horseshoe magnet experiments (Table 6-4). They additionally showed relatively low D.O.D. indices in comparison to those of the single magnet experiments. Their ability to orient to me was somehow compromised.

Fan Experiments

The presence of an operating fan in experiments testing the orientation response of flea larvae to a human stimulus was found to affect their ability to orient (Figure 6-7). Even the wind tunnel that was created to channel the wind flow also disrupted the orientation response regardless of whether the fan was "on" or "off" (Figure 6-7). Both conditions of "fan on" or "cover on" were enough to successfully confuse the flea larvae eliciting random movement in the petri dish as revealed by chi-square analysis in Table 6-5. No orientation toward or away from the fan resulted despite the very strong EM field it emanated (Figure 6-8).

The low chi-square values of Table 6-5 (4.78 to 7.34) contrast greatly with the control run (17.06) in which the fan was turned off and the cover on the wind tunnel was removed. This control experiment was almost identical to the one larva experiment of Figure 6-2, with the exception that a fan was placed at Section 2, but neither turned on nor plugged in. The presence of the unplugged fan had apparently no effect on the fleas.

Breakdown Data

Breakdown data refers to the data obtained by the breakdown of the entire hour's run into various increments. The breakdown data for all experiments not involving groups of larvae (50 or more larvae) will be collectively reviewed in this part. Data will be broken down into 10 minute increments. Therefore, the tables showing chi-square and D.O.D. index values will all be displayed in 10 minute increments. The individual graphs for each 10 minute block will be included in this chapter. However, breakdown data for 20 and 30 minute increments will be listed in the Appendix. This includes the associated radar graphs and all tables listing chi-square values and D.O.D. indices.

The graphical results of this breakdown analysis into 10 minute increments is represented by a host of figures starting with Figure 6-9 and ending with Figure 6-35. Each figure is clearly marked for the reader to help visualize the relative movement of fleas in the petri dish for each 10 minute block and for each experiment.

Tables 6-6 and 6-7 show the chi-square values and the D.O.D. indices for the Number Experiments, respectively. The same system applies to the Magnetic Experiments (Tables 6-8 and 6-9), the Magnet 10 Experiments (Tables 6-10 and 6-11), and the Fan 2 Experiments (Tables 6-12 and 6-13). The trend to notice is that the chi-square values are significant quite often during the first 10 minutes owing to the fact that the fleas are gently shaken at the beginning of each experiment and need several minutes to orient, at which point goodness of fit to a circle will gradually fall off. It should also be noted that some experiments such as "1 magnet at the top" and some of the fan experiments show randomness throughout the entire hour, if not most of the hour. There is no evidence from my research to support the idea that fleas orient only during certain times of the hour. Fluctuations are relatively low for virtually all experiments. Either the fleas are random, and therefore not orienting to anything during the experiment, or they orient quickly and remain so for the entire hour.

When the D.O.D. indices are summarized and graphed, some of these trends become visually apparent (Figure 6-36). As expected, all composite graphs show an increase in the D.O.D. index from the first 10 minutes to the second 10 minutes owing to the random distributions by which all experiments start out with (gentle shaking). There is a leveling off, sometimes an increase, at other times a decrease, of the D.O.D. indices from the second 10 minute period until the completion of the run.

Most of the composite graphs (Figure 6-36) show an increase of 2x or less from the first 10 minute period until the second 10 minute period. Although this is considered very good, one notable exception is the "10 larvae" composite graph which shows an impressive increase of 4x over the first 10 minute period. This figure even increases significantly by the end of the hour run and yet is composed of two experiments that were not significantly directive (Table 6-4). This composite graph serves to emphasize, along with the Height Experiments (Figure 6-1 and Table 6-1), the very strong enhancement of the orientation response when many larvae are involved.

Electromagnetic Field Experiment

Figure 6-37 shows the radial distribution of flea larvae in response to an electromagnetic field (n= 31) by graphing their final position at the end of one hour. The graphs clearly display a semi-random distribution (skewed toward one hemisphere) when the electromagnetic field is turned off, and an extremely directed response, directly away from the source of the field (Section 7), when the field is on.

Chi-square analysis for the "field off" experiment revealed a value of 28.13 which although significant at the p= 0.05 level, may be so because of its relatively low "n" of 12. Still, the chi-square value for the "field on" was a very high 226.35 showing that although both are not significantly random, the two cannot be considered the same. It is not until the D.O.D. indices are compared (the test had to be modified to show the degree of directivity toward Section 7) that the difference becomes more obvious. The D.O.D. index for the "field on" experiment was 302.58 making it comparable in directivity, although in a different direction, to some of the Height Experiments (Table 6-1). The D.O.D. index for the "field off" experiment (also tested for directivity toward Section 7) turned out to be an incredibly low value of 5.44.

The electromagnetic field intensity in the laboratory where most experiments were tested measured a constant 1.28 x 10^{-2} V/m. This level was only maintained in the center of the room. The baseline intensity was much higher in the room testing their response to electromagnetic fields. The baseline level in this room was over twice as high and measured 2.85 x 10^{-2} V/m, which was to be expected because the experiments could not be conducted in the center of the room, nor was the room as large as the main laboratory room where most of the experiments in this dissertation were conducted. The electromagnetic field intensity increased to 3.26 x 10^{-2} V/m when the field was applied. This is an increase of 4.1 x 10^{-3} V/m which is roughly two orders of magnitude higher than the minimum electric field observed to influence the behavior of the ray (10^{-5} V/m, Murray, 1965). No attempt was made to find the minimum electric (electromagnetic) field that influenced the flea larva's orientation behavior.

Competing human stimuli

The results of this experiment (n= 8) showed that the distance between flea larvae and a human stimulus can be affected by momentary movements on the part of the human stimulus toward the petri dishes such as would be caused by leaning over to record the locations of the ten flea larvae (Figure 6-38). I was the only one to lean over and record the data until the last eight minutes when the other individual began to record the flea larvae's relative location in the petri dish. The response of the flea larvae was immediate. Within two minutes (the difference between data recordings in my notebook) the flea larvae had begun to move in the other individual's direction and away from me. Only the last six minutes are displayed graphically and not the final eight minutes because the flea larvae were still on my side at time zero.

External Morphology

Gross Anatomy

The general body plan of the cat flea larva is maggot-like and composed of 14 segments (Figure 6-39). These segments become longer and thicker near the posterior end of the larva. The larva is eyeless and legless. The average length of a flea antenna was determined to be 57 μm. The base of the antenna was 38 μm, while the projecting spine constituted the remaining 19 μm.

Relatively long spines, or body setae project from the surface of the larvae stemming from the posterior end of each segment (Figure 6-39). The setae are arranged radially about each segment, and become gradually longer and thicker posteriorly The longer setae near the posterior end extend 350 μm or more from the base of the body. These body setae are often wider than the larva itself. All body setae are perfectly straight from base to tip.

The body setae are arranged in rows both laterally on a segment and longitudinally on the body. An individual seta therefore belongs to two different "antennal" arrays concurrently. There are no medial setae on either the dorsal or ventral surface of the flea larva.

Electron Micrographs

The base of the antennal seta is surrounded by four equally spaced spines (Figure 6-40). The base of the entire antenna is surrounded on only one hemisphere by five papillae (Figure 6-41). This same side reveals a surrounding cuticle of regular domes, while the opposing side displays an extremely smooth cuticle.

All the body setae reveal ridges on their surface under scanning electron microscopy (Figure 6-42), but the antennal seta appears perfectly smooth on its surface (Figure 6-40).

The cuticle of cat flea larvae is predominantly scale-like (Figures 6-43). These scales are conspicuously absent at the base of the body setae (Figure 6-42). This region devoid of scales is roughly circular to oval in shape. Additionally, this region appears to be as smooth as the area surrounding the antennal base on the side lying opposite the papillae.

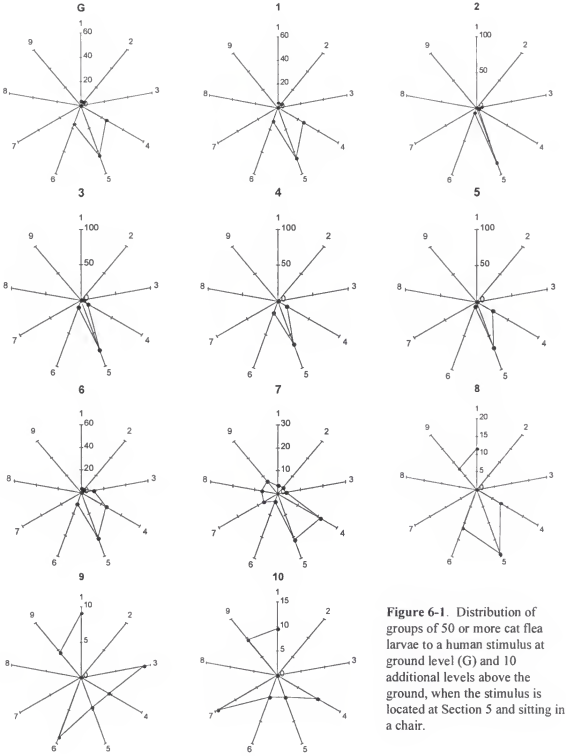
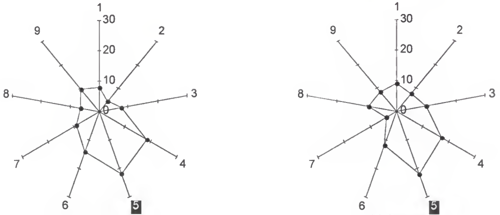
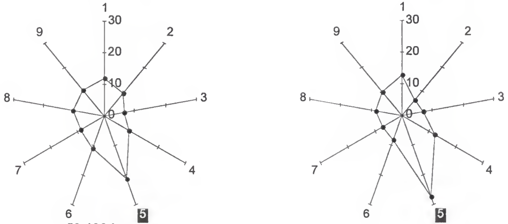


Figure 6-1. Distribution of groups of 50 or more cat flea larvae to a human stimulus at ground level (G) and 10 additional levels above the ground, when the stimulus is located at Section 5 and sitting in a chair.

One larva **Two larvae**



Five larvae **10 larvae**



50-100 larvae

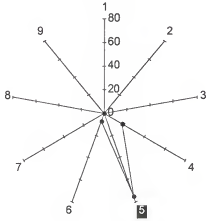
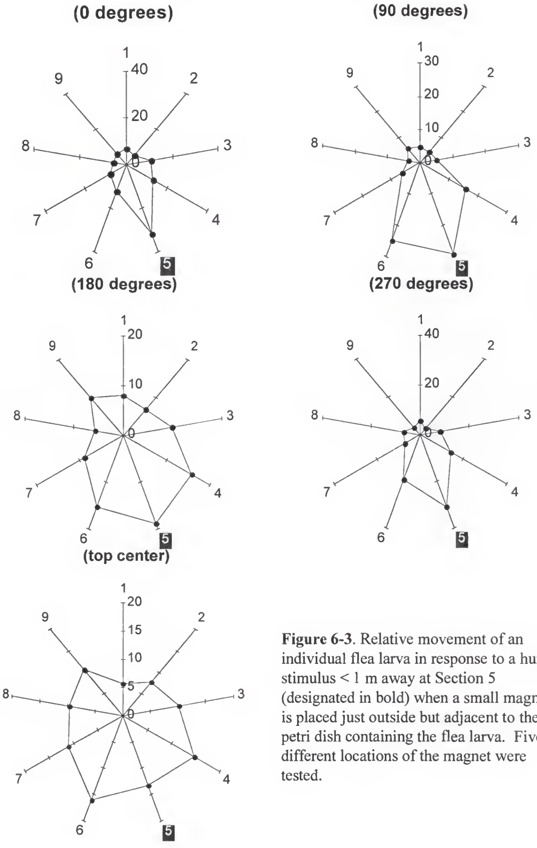


Figure 6-2. Relative movement of an individual flea larva, as well as 2, 5, 10 larvae, or a group of larvae (50-100) in response to a human stimulus < 1 m away at Section 5 (designated in bold). Last graph pulled from Figure 6-1 for comparison at the same height.



(0 degrees)

(90 degrees)

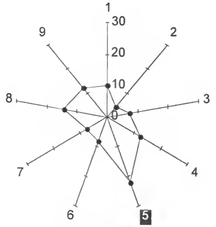
(180 degrees)

(270 degrees)

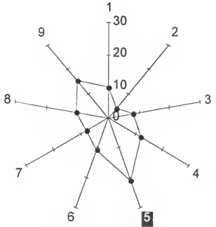
(top center)

Figure 6-3. Relative movement of an individual flea larva in response to a human stimulus < 1 m away at Section 5 (designated in bold) when a small magnet is placed just outside but adjacent to the petri dish containing the flea larva. Five different locations of the magnet were tested.

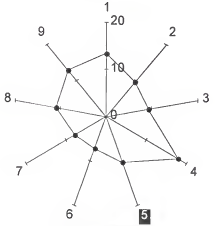
(0 degrees)



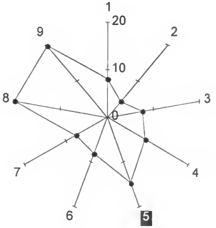
(90 degrees)



(180 degrees)



(270 degrees)



(top center)

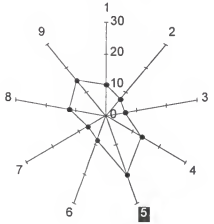
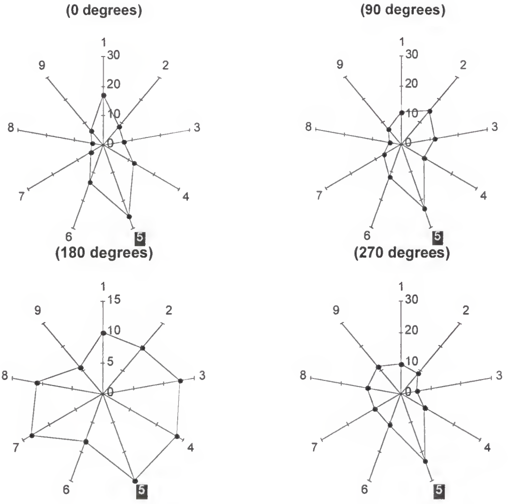


Figure 6-4. Relative movement of an individual flea larva in response to a human stimulus < 1 m away at Section 5 (designated in bold) when two small magnets (stacked) are placed just outside but adjacent to the petri dish containing the flea larva. Five different locations of the magnet were tested.



(0 degrees)

(90 degrees)

(180 degrees)

(270 degrees)

Figure 6-5. Relative movement of an individual flea larva in response to a human stimulus < 1 m away at Section 5 (designated in bold) when a large horseshoe magnet is placed just outside but adjacent to the petri dish containing the flea larva. Four different locations of the magnet were tested.

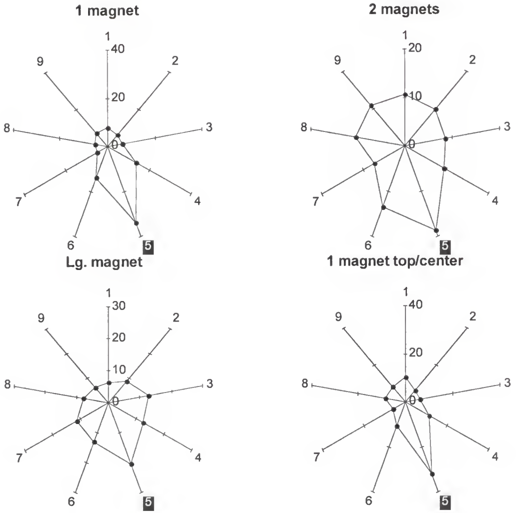
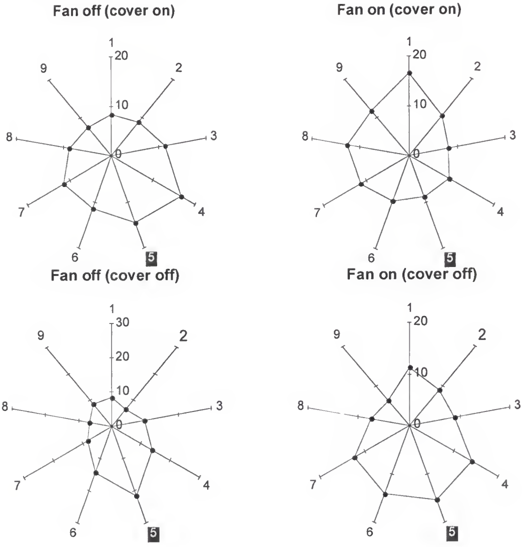


Figure 6-6. Relative movement of ten flea larva in response to a human stimulus < 1 m away at Section 5 and sitting in a chair. Response was tested with one small magnet, two small magnets (stacked), or a large horseshoe magnet all between the human stimulus located at Section 5 (designated in bold) and the petri dish (180°), as well as a single magnet on the top/center.



Fan off (cover on)

Fan on (cover on)

Fan off (cover off)

Fan on (cover off)

Figure 6-7. Relative movement of an individual flea larva in response to a human stimulus < 1 m away at Section 5 (designated in bold) and sitting in a chair. A flattened wind tunnel with a removable cover was used and a small fan was positioned at Section 2 irregardless of whether or not the fan was “on” or “off”.

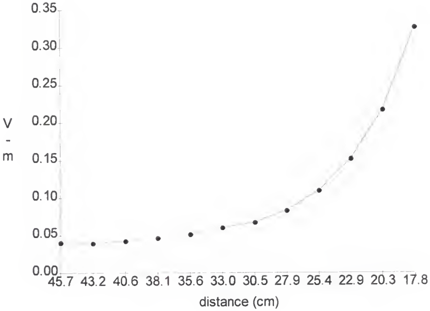


Figure 6-8. Electromagnetic field strength emanating from a fan, measured in Volts/meter, as a function of distance from the detector.

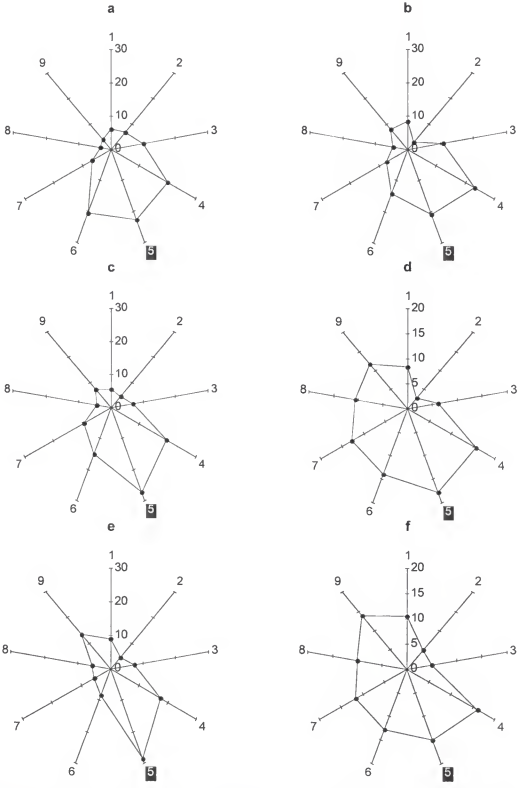


Figure 6-9. Number Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour. (n= 30)

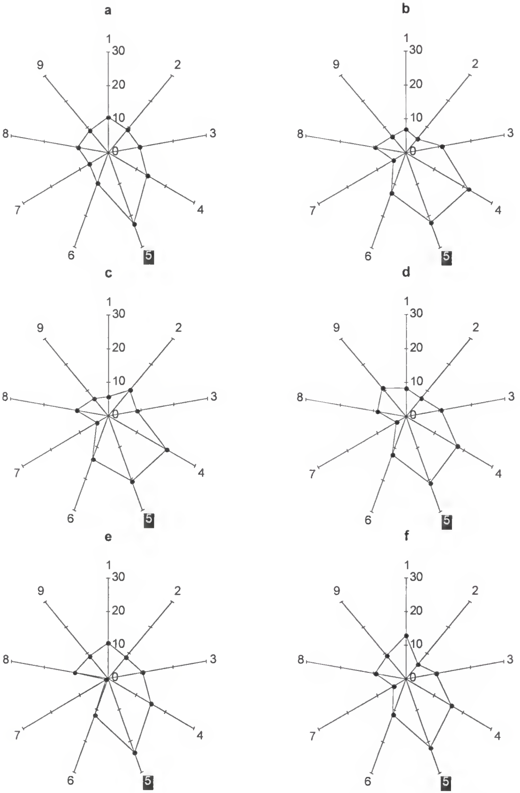


Figure 6-10. Number Experiment. Breakdown by 10 minute increments of two larvae's relative movement in a petri dish, over the course of one hour. (n= 30)

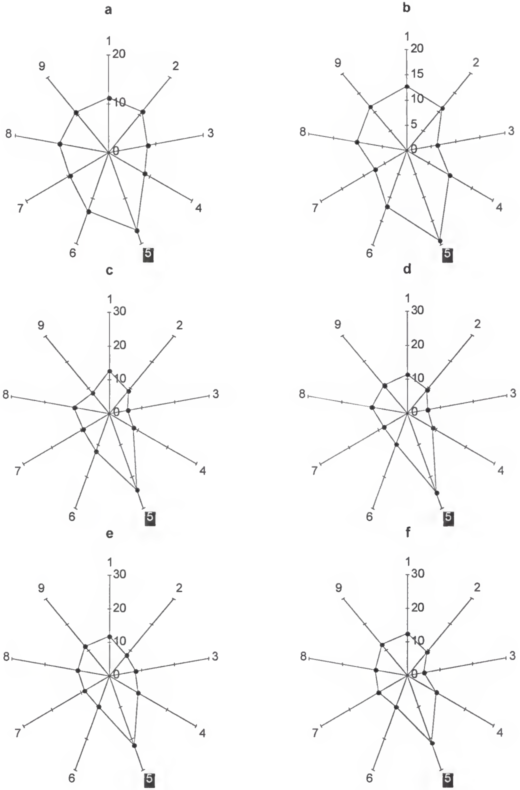


Figure 6-11. Number Experiment. Breakdown by 10 minute increments of five larvae's relative movement in a petri dish, over the course of one hour. (n= 30)

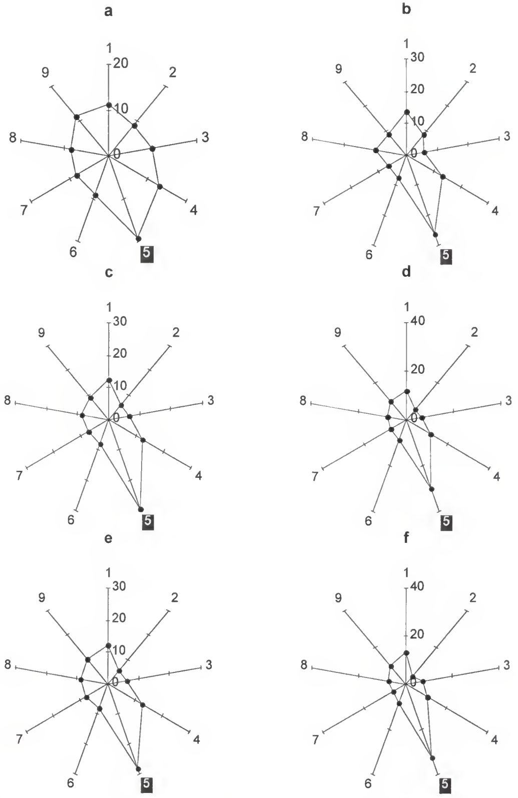


Figure 6-12. Number Experiment. Breakdown by 10 minute increments of ten larvae's relative movement in a petri dish, over the course of one hour. (n= 30)

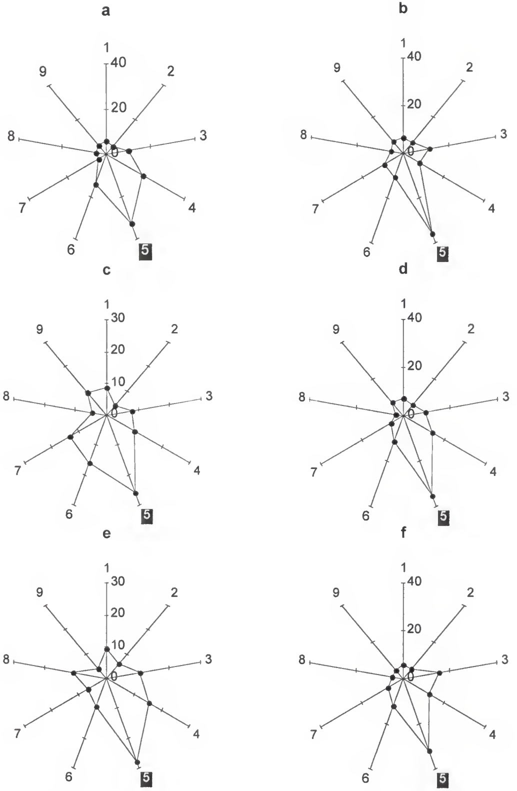


Figure 6-13. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small magnet is placed at 0 degrees. (n= 30)

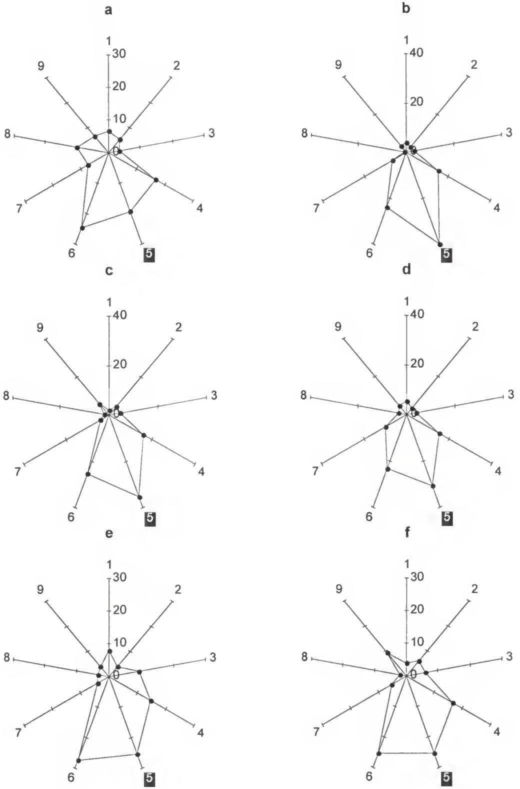


Figure 6-14. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small magnet is placed at 90 degrees. (n= 30)

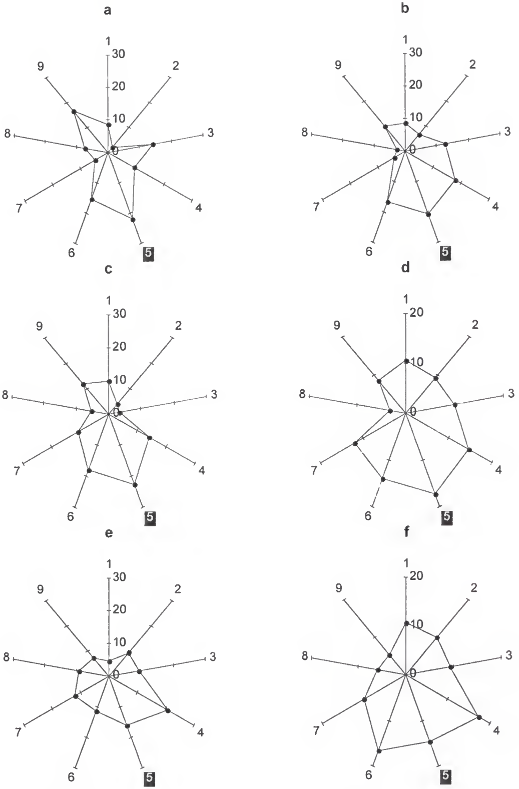


Figure 6-15. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small magnet is placed at 180 degrees. (n= 30)

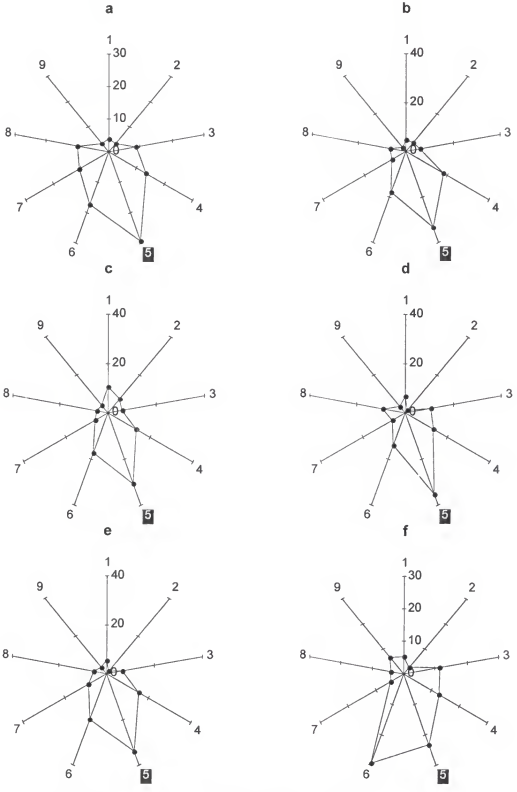


Figure 6-16. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small magnet is placed at 270 degrees. (n= 30)

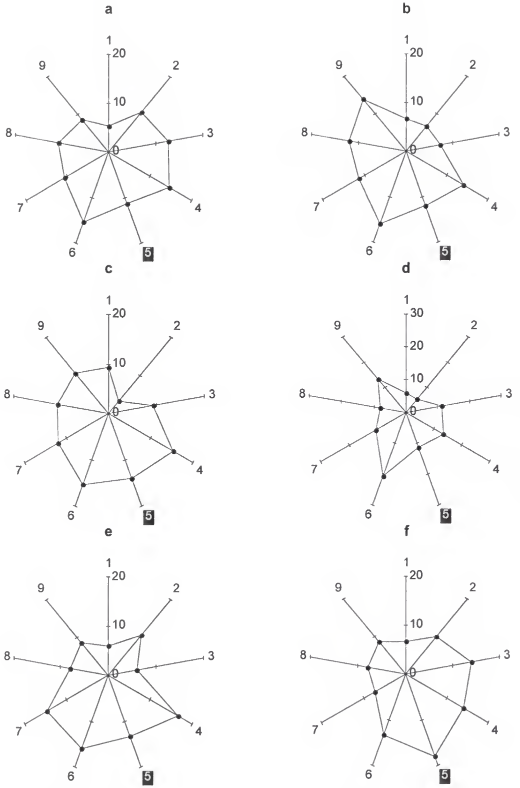


Figure 6-17. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small magnet is placed on the top/center of that petri dish. (n= 30)

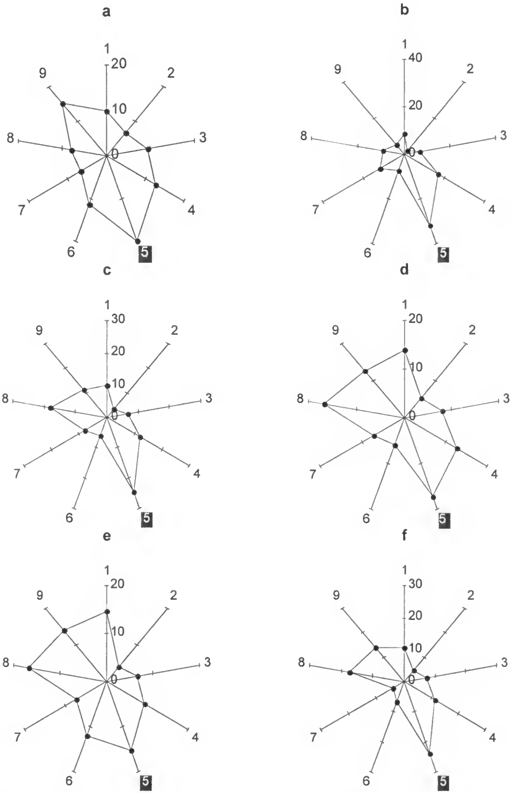


Figure 6-18. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when two small magnets, one on top of the other, are placed at 0 degrees. (n= 30)

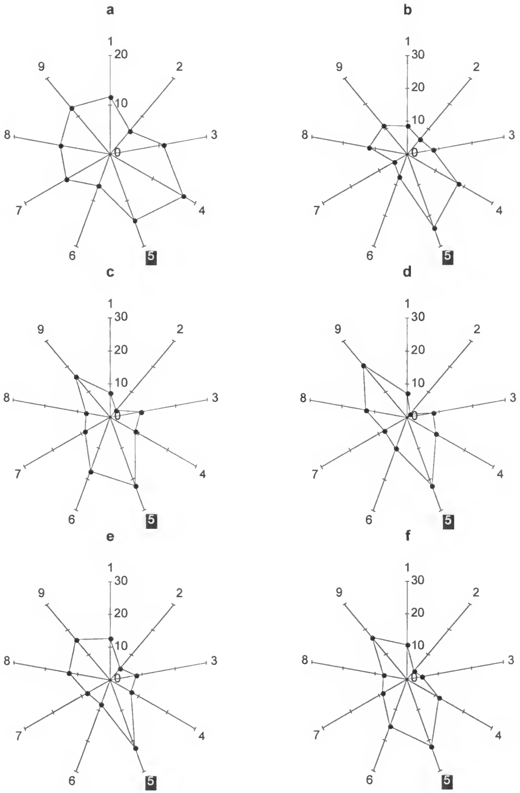


Figure 6-19. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when two small magnets, one on top of the other, are placed at 90 degrees. (n= 30)

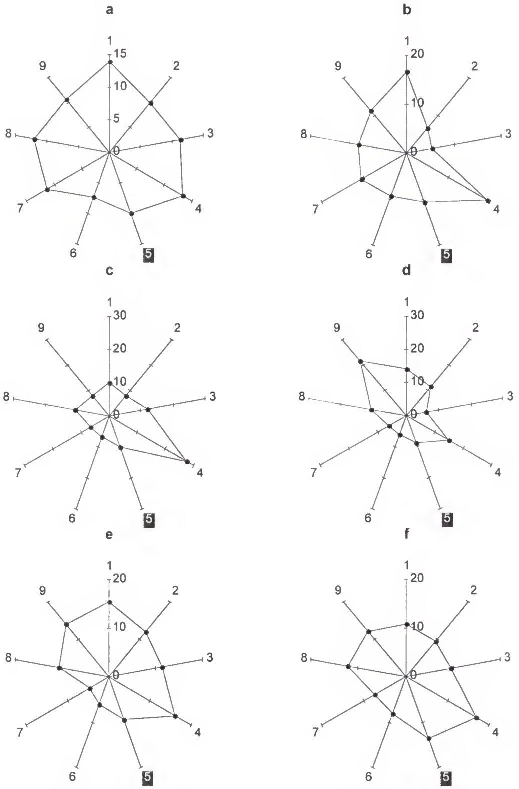


Figure 6-20. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when two small magnets, one on top of the other, are placed at 180 degrees. (n= 30)

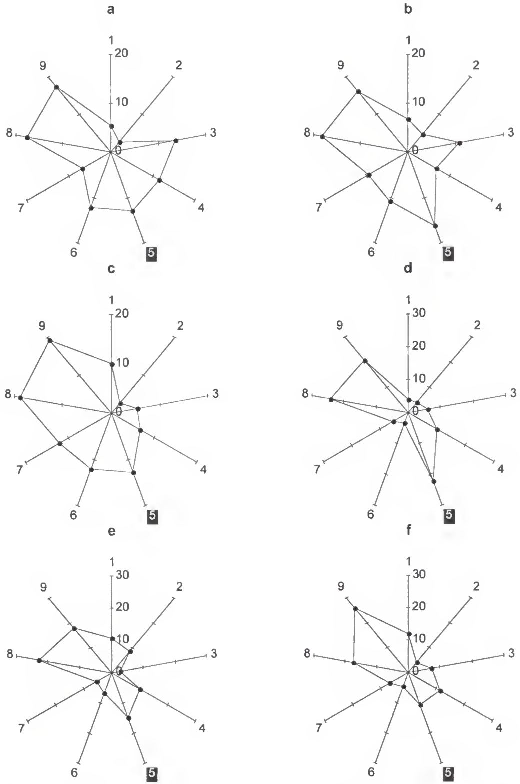


Figure 6-21. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when two small magnets, one on top of the other, are placed at 270 degrees. (n= 30)

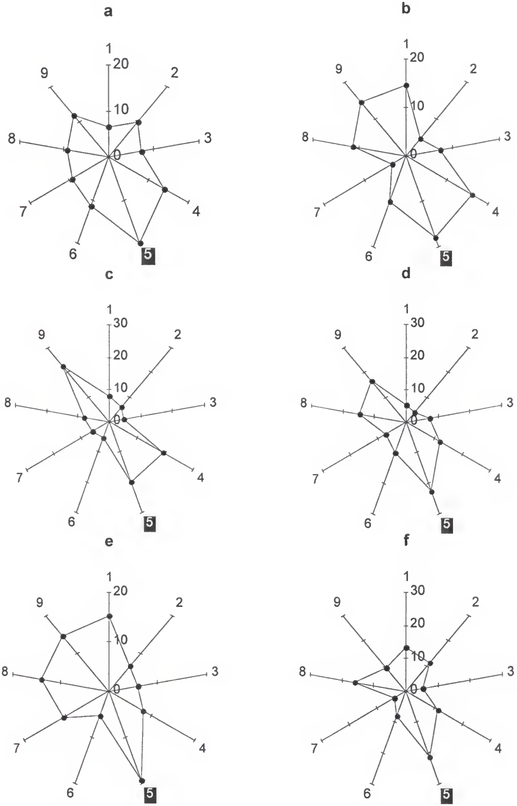


Figure 6-22. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when two small magnets, one on top of the other, are placed on the top/center of that petri dish. (n= 30)

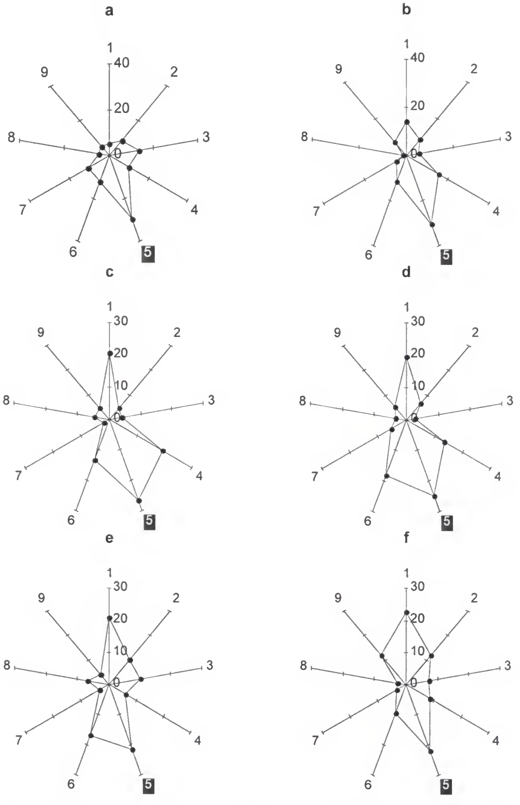


Figure 6-23. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a large magnet is placed at 0 degrees. (n= 30)

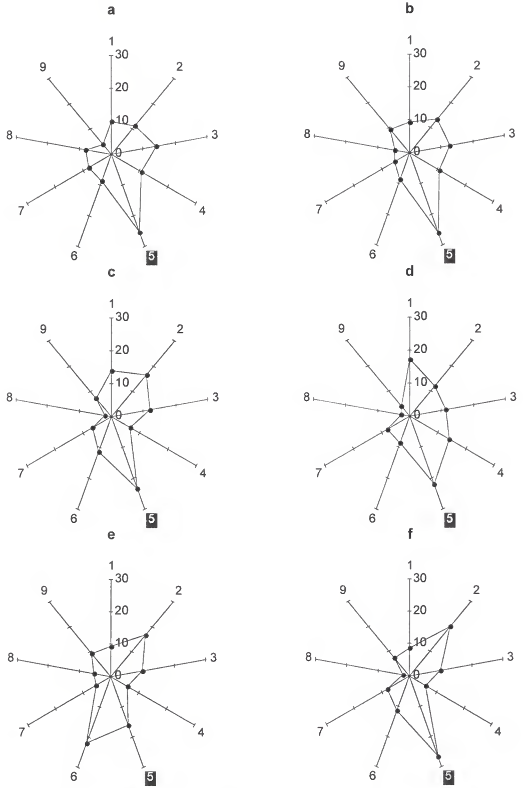


Figure 6-24. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a large magnet is placed at 90 degrees. (n= 30)

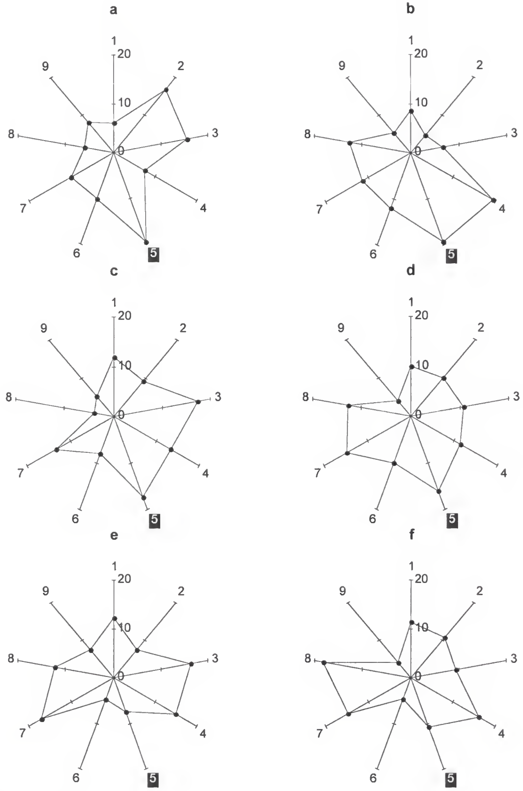


Figure 6-25. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a large magnet is placed at 180 degrees. (n= 30)

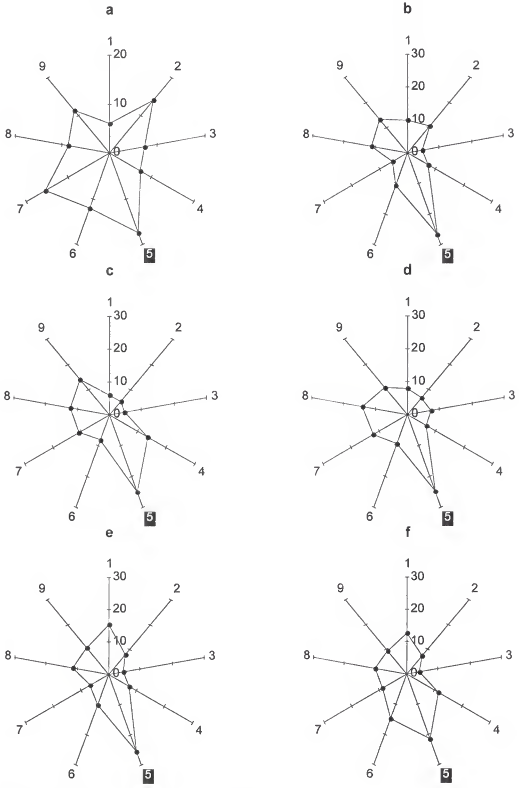


Figure 6-26. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a large magnet is placed at 270 degrees. (n= 30)

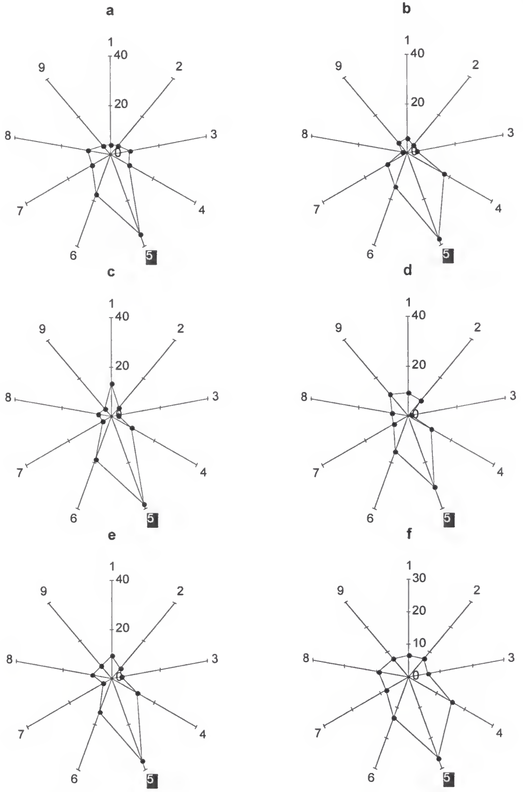


Figure 6-27. Magnet Experiment. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when four small magnets are adjacently placed, all under the petri dish. (n= 30)

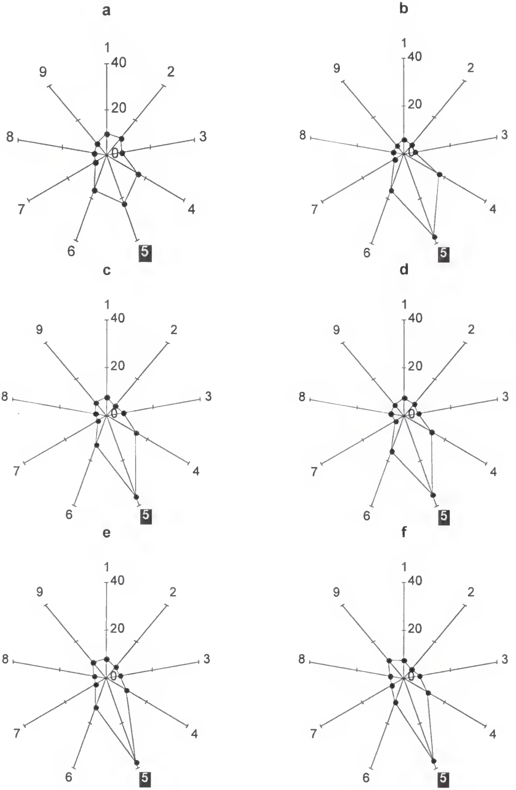


Figure 6-28. Magnet 10 Experiment. Breakdown by 10 minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when a small magnet is placed at 180 degrees. (n= 30)

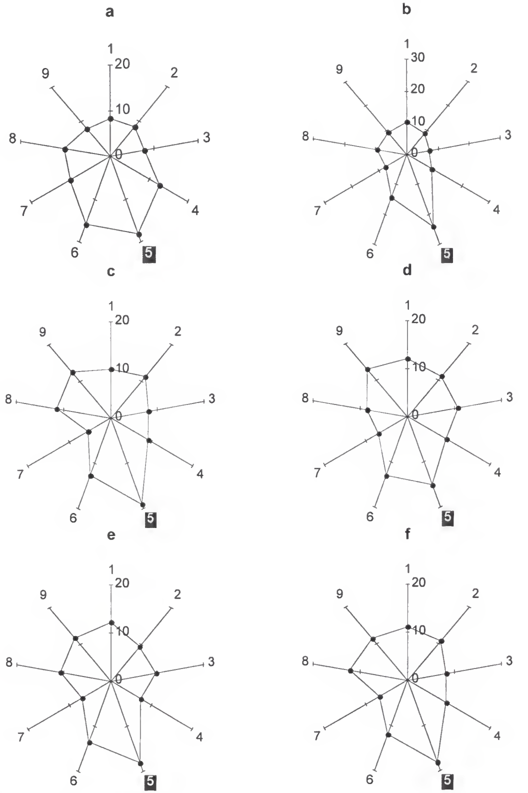


Figure 6-29. Magnet 10 Experiment. Breakdown by 10 minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when a two small magnets are placed one on top of the other, at 180 degrees. (n= 30)

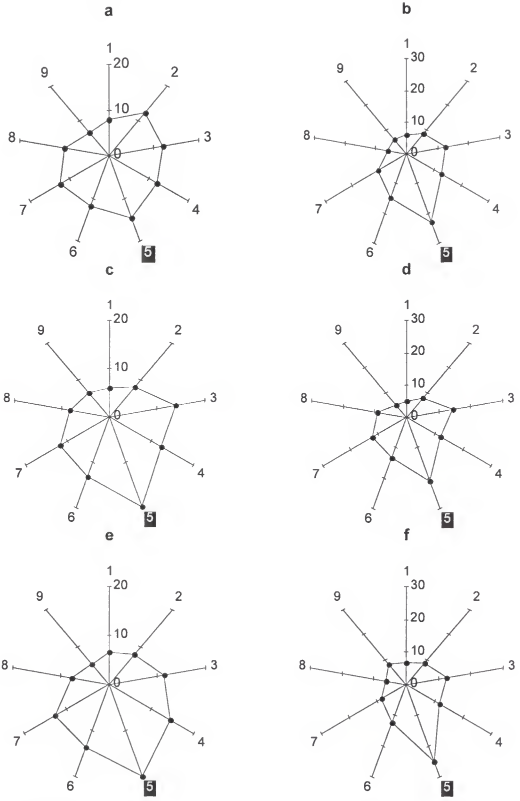


Figure 6-30. Magnet 10 Experiment. Breakdown by 10 minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when a large magnet is placed at 180 degrees. (n= 30)

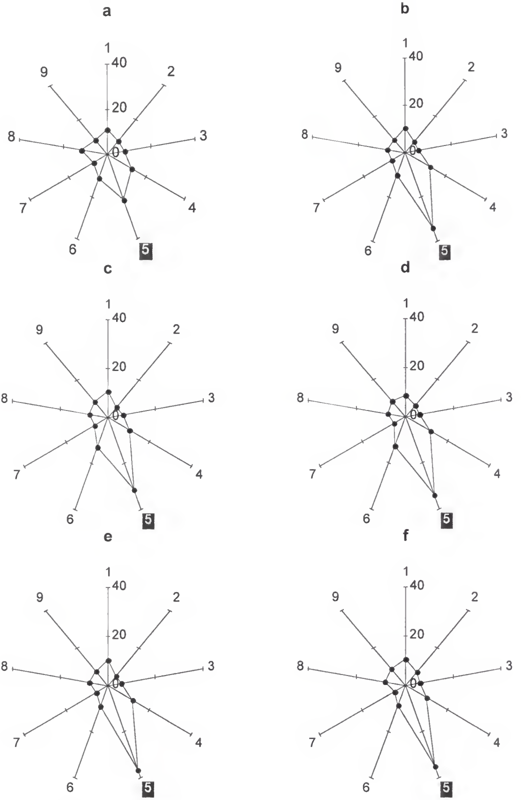


Figure 6-31. Magnet 10 Experiment. Breakdown by 10 minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when a small magnet is placed on the top/center of the petri dish. (n= 30)

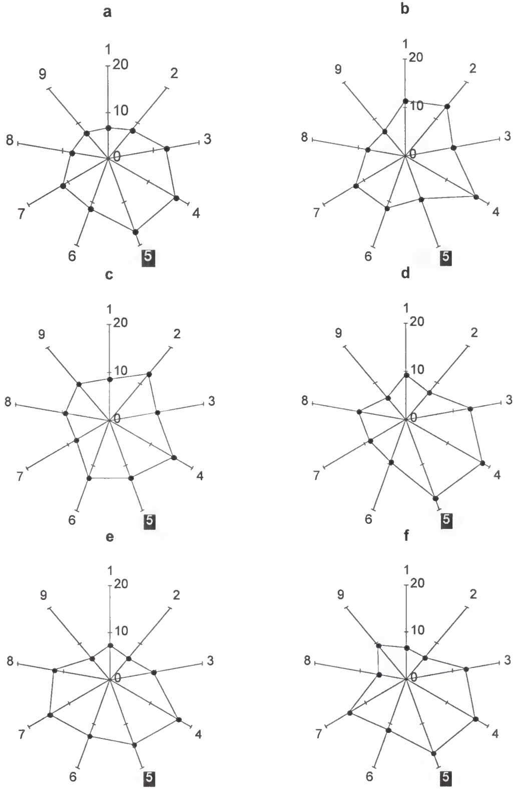


Figure 6-32. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan was turned off, and the cover was on. (n= 30)

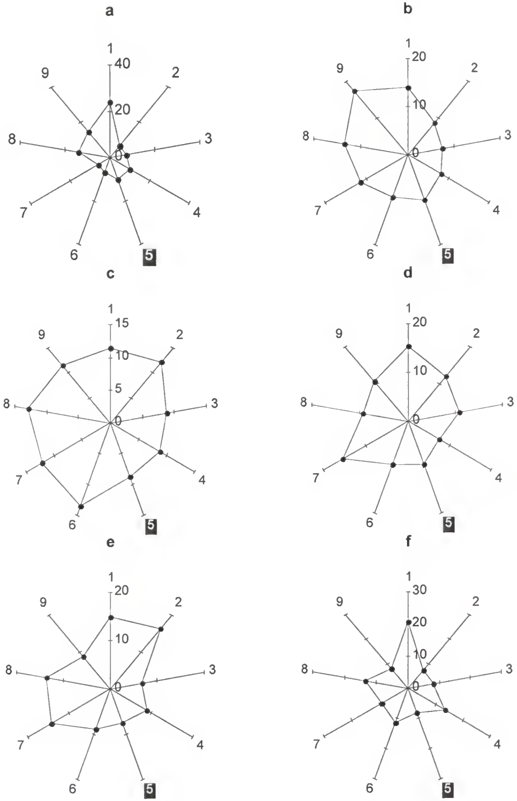


Figure 6-33. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan was turned on, and the cover was on. (n= 30)

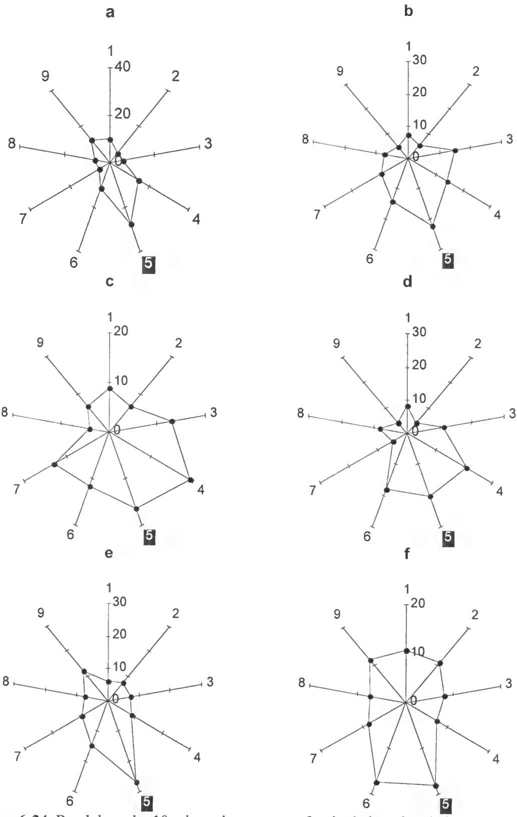


Figure 6-34. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan was turned off, and the cover was off. (n= 30)

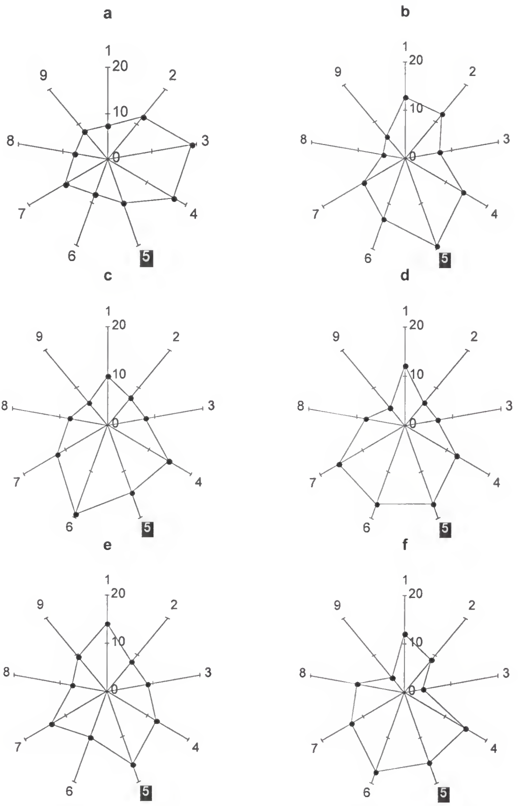


Figure 6-35. Breakdown by 10 minute increments of a single larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan was turned on, and the cover was off. (n= 30)

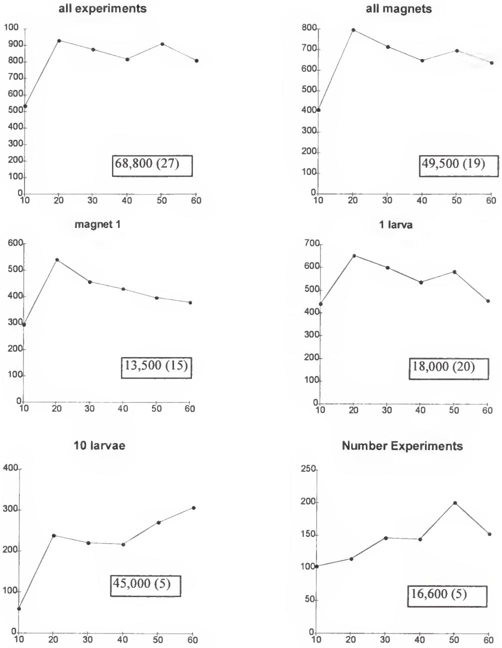


Figure 6-36. Degree of directivity (D.O.D.) composite graphs, plotting D.O.D. indices for all of the experiments whereby data acquistion was recorded every 2 minutes. All of the experiments (all experiments), all experiments involving a magnet of any type (all magnets), all experiments involving a magnet and only one larva in the petri dish (magnet 1), all experiments involving only one larva in the petri dish (1 larva), all experiments whereby 10 larvae were used concurrently, and all of the Number Experiments are shown. All y-axes are cumulative D.O.D. indices, while all x-axes are minutes during the hour long experiments. All boxes contain the total number of data points by which the graph is composed, as well as the number of experiments involved in the designated group (in parenthesis).

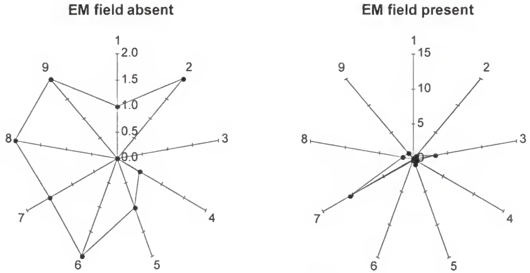
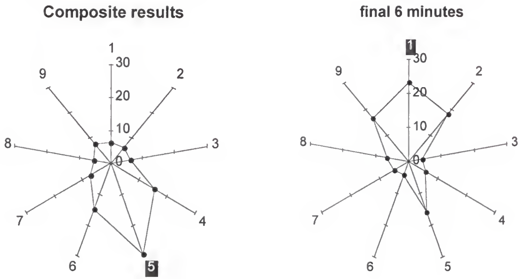


Figure 6-37. Final location of a group of flea larvae, after the course of one hour, in response to an artificial electromagnetic field turned "on" and "off" (n= 19 and 12, respectively). The field originates from two general directions, those directions roughly being Sections 2 and 3.


Composite results

final 6 minutes

Figure 6-38. Relative movement of 10 flea larvae in a petri dish, over the course of one hour, when competing human stimuli are located at both Section 5 and Section 1 (n= 8). Data acquisition was accomplished by leaning over the petri dishes for a better view. A switch was made such that the individual at Section 1 began to lean over the petri dishes with only eight minutes remaining in the experiment while the individual at Section 5 remained sitting upright. The relative movement of the fleas is shown therefore for the final six minutes.

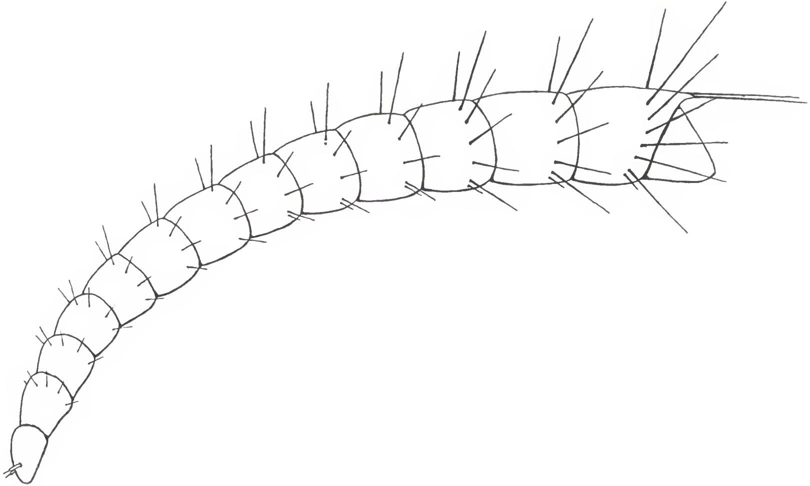


Figure 6-39. Diagrammatic picture of a cat flea larva showing body segmentation, body setae, and antennae.

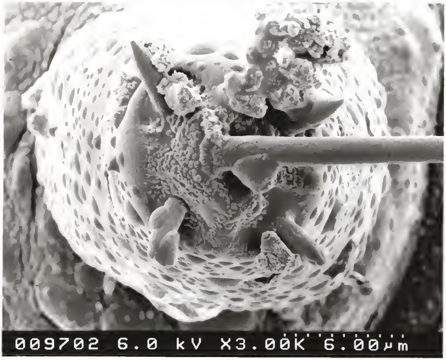


Figure 6-40. Scanning electron micrograph of a cat flea antenna, showing close-up of antennal seta with four equally spaced spines at the base.

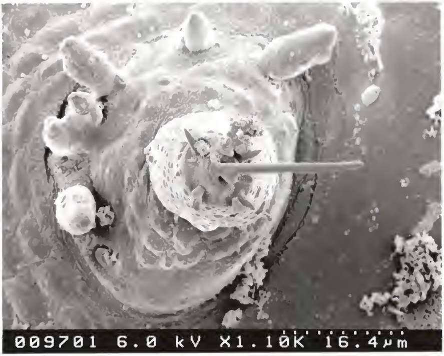


Figure 6-41. Scanning electron micrograph of a cat flea antenna, showing close-up of the antennal base and the five papillae that surround only one hemisphere.

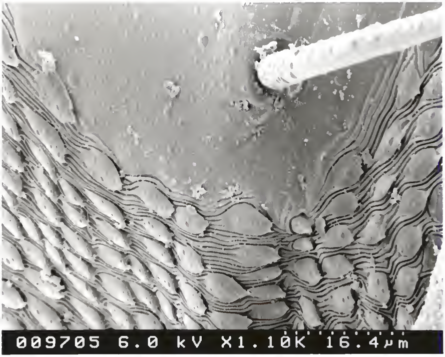


Figure 6-42. Scanning electron micrograph of a cat flea, showing a close-up of one of the body seta. Note the ridged texture of the seta, and the conspicuous absence of scales surrounding the setal base.

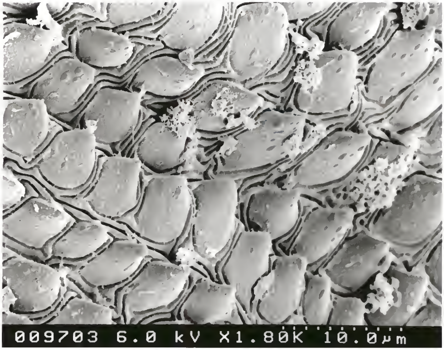


Figure 6-43. Scanning electron micrograph of a cat flea, showing a close-up of the cuticular topology of the body proper.

Table 6-1. Height Experiments. Chi-square values testing goodness of fit to a circle, and degree of directivity (D.O.D.) index values for testing level of directivity toward Section 5 are shown.

Level	Chi-square	D.O.D. index
Ground	168.00	110.48
1	179.17	130.42
2	517.60	497.51
3	428.06	364.80
4	326.15	241.80
5	375.26	280.87
6	151.66	101.04
7	43.88	57.38
8	52.51	45.38
9	46.07	15.15
10	42.18	22.45

Table 6-2. Number Experiments. Chi-square values testing goodness of fit to a circle, and degree of directivity (D.O.D.) index values for testing level of directivity toward Section 5 are shown. Chi-square values in bold indicate a goodness of fit to a circle at p= 0.05.

Number of larvae	Chi-square	D.O.D. index
1 larva	24.87	13.89
2 larvae	21.32	20.95
5 larvae	**12.48**	24.24
10 larvae	30.76	50.18

Table 6-3. Magnet Experiments. Chi-square values testing goodness of fit to a circle, and degree of directivity (D.O.D.) index values for testing level of directivity toward Section 5 are shown. Chi-square values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiment	**Location**	**Chi-square**	**D.O.D. index**
1 magnet	**0**	49.07	49.30
	90	70.01	37.16
	180	**14.69**	6.17
	270	59.31	37.35
	Top/center	**7.77**	2.42
2 magnets	**0**	19.60	28.16
	90	17.01	18.00
	180	**7.87**	17.40
	270	22.50	8.54
	Top/center	**15.38**	22.70
Lg. magnet	**0**	35.20	33.93
	90	22.61	28.15
	180	**6.30**	6.38
	270	17.63	33.10
4 adjacent magnets	**Under**	61.84	63.75

Table 6-4. Magnet 10 Experiments. Chi-square values testing goodness of fit to a circle, and degree of directivity (D.O.D.) index values for testing level of directivity toward Section 5 are shown. Chi-square values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiment	**Chi-square**	**D.O.D. index**
1 magnet	61.10	63.22
2 magnets	**8.05**	13.83
Lg. magnet	**14.10**	8.93
1 magnet top/center	47.51	67.85

Table 6-5. Fan 2 Experiments. Chi-square values testing goodness of fit to a circle, and degree of directivity (D.O.D.) index values for testing level of directivity toward Section 5 are shown. Chi-square values in bold indicate a goodness of fit to a circle at p= 0.05.

Cover	**Fan**	**Chi-square**	**D.O.D. Index**
On	**Off**	**6.59**	3.74
On	**On**	**4.78**	0.69
Off	**Off**	17.06	12.23
Off	**On**	**7.34**	2.08

Table 6-6. Number Experiments. Breakdown analysis into 10 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Number	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
1 larva	43.44	35.45	45.64	16.15	43.50	**11.44**
2 larvae	16.00	32.13	26.26	21.10	26.89	20.92
5 larvae	**4.90**	**9.73**	20.69	21.69	**13.53**	**13.96**
10 larvae	**8.48**	28.73	37.97	39.78	34.32	51.63

Table 6-7. Number Experiments. Breakdown analysis into 10 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Number	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
1 larva	13.27	16.28	24.81	6.86	50.14	7.03
2 larvae	23.98	21.84	18.95	19.32	31.54	21.28
5 larvae	10.14	16.59	36.29	43.61	26.08	25.60
10 larvae	14.33	48.60	60.07	62.02	53.74	79.46

Table 6-8. Magnetic Experiments. Breakdown analysis into 10 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiment	**Location**	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
1 magnet	**0**	65.20	65.84	32.64	66.56	36.56	55.28
	90	38.80	125.12	102.48	71.76	63.28	59.20
	180	29.12	28.88	30.24	**11.84**	16.32	**13.28**
	270	49.92	73.84	52.64	72.48	78.24	63.04
	T/C	**6.56**	**8.64**	**10.08**	**15.36**	**12.64**	**10.80**
2 magnets	**0**	**13.76**	56.48	31.44	**14.96**	**14.24**	30.56
	90	**8.34**	28.08	27.01	30.96	21.17	26.08
	180	**2.80**	**14.08**	29.68	19.40	**11.12**	**6.25**
	270	19.40	16.61	23.20	54.57	29.68	34.88
	T/C	**11.68**	19.28	38.40	26.24	17.60	20.72
Lg. magnet	**0**	41.36	53.73	59.76	48.25	35.67	36.80
	90	25.92	28.48	29.36	27.36	24.64	41.52
	180	18.01	21.52	16.64	**8.52**	**14.33**	16.39
	270	**11.52**	30.40	28.52	23.68	27.98	17.76
4 adj. magn.	**Under**	67.68	88.72	93.20	49.36	72.00	31.68

Table 6-9. Magnetic Experiments. Breakdown analysis into 10 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Experiment	**Location**	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
1 magnet	**0**	46.88	89.21	28.59	69.81	41.01	49.92
	90	24.81	72.41	57.27	37.01	33.41	29.13
	180	23.36	12.60	19.83	3.07	11.30	4.57
	270	30.81	43.73	44.42	62.33	44.50	37.22
	T/C	2.61	4.62	2.14	11.50	6.34	6.09
2 magnets	**0**	14.31	61.96	46.43	19.35	7.99	46.40
	90	14.10	39.17	23.01	25.71	37.38	21.32
	180	5.37	18.44	57.46	15.10	18.64	11.93
	270	2.68	12.39	9.10	54.75	17.19	9.94
	T/C	13.00	18.19	40.81	26.05	33.40	33.41
Lg. magnet	**0**	44.04	53.39	41.85	32.91	36.75	36.44
	90	37.38	43.66	36.94	22.13	34.70	53.23
	180	20.84	13.09	11.06	5.45	22.66	19.80
	270	15.29	58.99	38.44	46.30	52.69	20.86
4 adj. magn.	**Under**	68.31	65.62	97.12	61.78	81.84	30.15

Table 6-10. Magnet 10 Experiments. Breakdown analysis into 10 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiment	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
1 magnet	25.51	86.25	71.95	67.72	75.53	69.84
2 magnets	**9.93**	20.27	**10.35**	**4.69**	**8.40**	**7.57**
Lg. magnet	**4.38**	21.88	**13.75**	18.47	**15.48**	23.65
1 magnet t/c	**13.96**	57.44	45.97	57.65	70.47	60.86

Table 6-11. Magnet 10 Experiments. Breakdown analysis into 10 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Experiment	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
1 magnet	17.75	67.52	74.11	66.75	95.41	89.97
2 magnets	7.29	31.26	17.87	6.47	17.01	13.93
Lg. magnet	1.14	13.23	7.40	9.92	5.99	25.58
1 magnet t/c	19.06	77.83	61.69	72.78	99.31	98.58

Table 6-12. Fan 2 Experiments. Breakdown analysis into 10 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Cover	**Fan**	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
On	**Off**	**10.86**	**6.50**	**4.23**	**13.22**	**11.77**	**13.47**
On	**On**	24.58	**7.87**	**2.47**	**5.52**	**9.50**	**13.47**
Off	**Off**	35.76	23.51	17.21	33.77	30.41	**11.93**
Off	**On**	**12.75**	**15.25**	**13.92**	16.66	**6.67**	16.69

Table 6-13. Fan 2 Experiments. Breakdown analysis into 10 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Cover	**Fan**	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**
On	**Off**	4.79	7.52	3.42	12.00	3.37	4.17
On	**On**	3.47	1.57	4.86	4.11	4.06	4.83
Off	**Off**	40.95	10.87	6.29	12.94	39.42	19.72
Off	**On**	13.94	9.26	6.81	7.44	5.76	9.04

CHAPTER 7
DISCUSSION

The positive orientation reaction toward a human being has been well-documented in this dissertation research. The apparent necessity of a cat flea larva to locate a host is most likely the primary behavior of this insect and the ability to locate a human only a secondary response. There is a very strong orientation, which qualifies it as a *taxis* response. However, *anthrotaxis* (meaning orientation toward man) cannot be justified as the correct description for this behavior, because it is felt that the "anthrotaxis" behavior observed is only a side effect based upon misidentification on the part of the flea. In nature, the only moving animal in the immediate vicinity of a searching flea larva will almost certainly be its host.

The prohibitive cost of using live animals in this research, as well as the difficulties in keeping the animal relatively motionless throughout an experiment, meant that the characterization of this response would have to be first carried out upon a willing human volunteer. Once the behavior had been sufficiently characterized and understood, animals could then be brought in for comparative purposes. This is a line of inquiry that other researchers are invited to carry out.

A behavioral response for any animal is a complicated reaction that is often dependent upon many constituents that collectively make up the observed behavior. A novel behavior has been noted with cat flea larvae during this research, but the individual mechanisms and how they interact is a question that could not be answered during this investigation.

The determinants of this taxis behavior are not well understood, even at the conclusion of this research. It was not possible to ascertain whether the individual flea operated independently or whether their inclusion within a group of larvae increased their ability to locate a potential host. Some birds show a relatively poor orientational ability (not homing pigeons, however) but when flying in a group or flock, the groups ability to orient far exceeds that of the individual (Naumov and Il'ichev, 1965). The ability of groups of flea larvae to orient to me and then remain so for hours may be related to the similar and remarkable synergistic effect found in birds. Since aggregations of flea larvae always formed before an orientational behavior was observed, the fleas were forced to move toward me as a group, and sometimes in an "amoeboid" fashion. This observation is in stark contrast with ticks who generally ceased "searching" behavior once they joined an aggregation of other ticks (Norval et al., 1989). Furthermore, ticks were attracted to dry ice (Harris and Burns, 1972; Burns and Melancon, 1977; Norval et al., 1987; 1989) but not to human beings (Norval et al., 1987). Many carbon dioxide traps for ticks (Garcia, 1962; Wilson et al., 1972; Eads et al., 1982; Gray, 1985) have been used effectively in the field. Apparently, the orientation behavior in ticks, although similar in the sense that both orient to animals who directly or indirectly provide their nourishment, was not so closely related to that of flea larvae.

The orientation response was also not hunger dependent. Healthy larvae were removed from the sand medium where there was an abundance of food. All the larvae were probably satiated when removed for the experiments, and yet the orientation response was repeatedly observed under just these conditions. Larvae that had been removed from any food source for 6 to 24 hours, however, did not display an increased ability to locate a human stimulus as might be expected, but instead appeared more lethargic and unresponsive, indicative of starvation. This is in contrast to mosquitoes who become immediately unresponsive to odors associated with mammalian hosts after a blood meal (Klowden, 1990).

The nature of the orientation behavior in fleas may take many more years of study before we understand it enough to formally give it a name. My investigation began with a behavioral approach and then moved to a morphological approach when it became apparent that electromagnetic fields influence cat flea larvae and may very well be playing a role in their observed orientation behavior. The flea's antennae, as well as their body setae, and any speculative internal receptors or mechanisms are all quite possibly involved when speculating on the mechanisms underlying this fascinating behavior. Several possibilities follow as to how the cat flea may be able to accomplish this complex orientational response to human beings.

The Antennae

Larvae of the cat flea are only a few millimeters long. Even for their size, they have relatively small antennae (Figure 6-38). Their antennae have no pectination which means the antennal surface area is extremely reduced. Attraction of molecules to its surface might be mediated by electrostatic attraction as mentioned in Chapter 2 when it was shown by Warnke (1989a) that charged particles selectively adhere to insect sensilla when the cuticle itself is charged. Electrostatic attraction can occur on the cuticle by the maintenance of a charge separation between the internal milieu of the spine and the external environment. Logic dictates that any living insect will have this charge separation. Therefore, one may assume, by reasoning through the physics, that the cuticle is charged and that electrostatically charged particles will show some attraction to the cuticular extensions (due to the "point effect" as I have mentioned in Chapter 2) such as spines, setae, and various other insect sensilla. Charged particles would form a thin monolayer on the antennae (Callahan, 1975b) and the modulation or stimulation of this molecular monolayer could possibly increase coherent emissions 10-fold as Callahan (1975a) has shown with the cabbage looper pheromone.

Cabbage looper moths vibrate both their antennae and their wings at approximately 50 Hz. Stimulation by either one of these modalities or quite possibly even the 60 Hz modulation frequency created by the lighting in almost any laboratory in the United States might be a sufficient "pumping" source for stimulating molecules to emit. All of the experiments in this dissertation were conducted indoors, and therefore, only artificial lights were used for illumination. The lighting may be an important modulating/pumping frequency when the antennae are excised from insects and immobile in modeling clay, such as in electrophysiological laboratory experiments.

Electromagnetic frequencies are stimulated to emit from all molecules above 0° Kelvin. These infrared frequencies (see Chapter 2) travel through space until they are absorbed by an antenna or the atmosphere. The projecting spine at the tip of the antenna is long and thin, and like all insect cuticular structures, is covered with a waxy layer. This makes it a dielectric antenna. The presence of four, equally spaced spines at the base of the central spine bear a striking resemblance to man-made antennae where the central receiver is surrounded by modifiers that will take on the roles of either directors or reflectors depending upon physical and radiative circumstances.

The reception of electromagnetic frequencies from the atmosphere or from a stimulated molecular monolayer spread over the antennae can only be achieved by antennae tuned in to these frequencies. All insect spines are dielectric antennae. This statement can be made because all insect spines possess the characteristics of a good dielectric antenna, such as impedance matching, high gain, and a wax layer. However, it is not conclusively known whether the EM frequencies undoubtedly received by these spines are in turn *perceived* by the insect.

Antennae are collectors and amplifiers of frequencies to which they are tuned. For this reason, antennae are capable of detecting certain wavelengths from a sea of wavelengths by virtue of the fact that all the "noise" coming from this atmospheric sea simply cannot all be received by a given antenna. The antenna amplifies the Rayleigh center line (coherent line) by selectively tuning to that frequency. This process bears some functional resemblance to center surround antagonism which involves horizontal cells exhibiting lateral inhibition (Barlow, 1982). Center surround antagonism is found very commonly in all sensory pathways and serves to emphasize contrast while sacrificing uniformity of the actual image. The antenna is tuned to its particular frequency and amplifies the center line, thus effectively reducing frequencies adjacent to the tuned frequency (although not actively such as occurs in the retina). The reduction in frequencies comes about through the inherent properties of an antenna whereby an antenna is selectively tuned to a primary frequency and also to multiples of the frequency (Chapter 2). For example, a given antenna tuned to a frequency of 20 cm might be able to detect 40 cm wavelength radiation better than 17 cm wavelength radiation. The neighboring peaks would be inherently reduced to a virtually non-detectable level.

Many papers have reported various responses of insects to EM frequencies as well as its components, electrical and magnetic fields, and I have already outlined these findings in Chapter 2. Established sensory organs (pits) responding to EM frequencies, specifically in the infrared, have been shown by Evans (1966b) and the bottom of these pits are covered with closely spaced bulbs. There are no other structures in this pit which means, by default, that these bulbs are almost certainly the infrared receptors. Electromagnetic receivers on insects have all pointed toward an *external* modality, such as pits (Grant, 1948; Evans, 1966b) or setae (Callahan, 1967) since EM frequencies much shorter than radio waves will not penetrate the cuticle (Presman, 1970).

The antenna of the cat flea larva is surrounded at its base by 5 papillae. These papillae are only found on the outer side of the antenna, that is facing away from the center or midline. The mirror image is formed by the other antenna. This arrangement strongly suggests some directional function. These papillae might be modifiers for the central antenna proper for receiving and determining the direction of incoming EM frequencies. In reference to insect sensilla coeloconica on moths, the spacing of each dielectric picket might act as a reflector or phasing bar for incoming radiation (Callahan and Lee, 1974). Because the papillae are shorter than the central receiver, the antenna proper, the papillae probably act as directors and not reflectors (Smith, 1988). What occurs then is the altering of the central receiver's radiation lobe. The lobe will be skewed toward the side of the directors. The presence of these papillae on only one side could adjust the shape and direction of the radiation lobe which effectively directionalizes the antenna.

A similar arrangement repeats itself at the distal end of the antenna. The tip of the antenna has a projecting spine which is itself surrounded by its own "papillae". Although these papillae are more spine-like (Figure 6-10) there are only four of them, and they position themselves at the four corners (North, South, East, and West, figuratively speaking) at the base of the spine. Their presence at the base suggests an electromagnetic receiving function whereby the main spine may be acting as a central receiver, and the surrounding spines would be functioning as modifiers of the central receiver. These modifiers would also be directors, but because of the equidistant positions of the directors, unidirectionality cannot be expected. Instead, they may be omnidirectional. If these spines are not innervated, then they would be parasitic, and it is known that the adding of parasitic directors or reflectors can increase both gain and front-to-back ratio (Figure 7-1) for a specific frequency (The ARRL Antenna Book, 1974).

Electromagnetic antennae, and especially dielectric waveguides, have functions dictated by the morphology of the antenna including the "morphology" of structures adjacent to them. The scatter surfaces surrounding them, the presence of parasitic elements posing as directors or reflectors, and the shape and surface structure of the central receiver all play a role in how radiation is received. In relation to this, a striking contrast exists on flea larvae which concerns the setae on the body, and the seta on the antennae. As I have mentioned in Chapter 6, the antennal seta is smooth (Figure 6-11). The smooth surface will affect the way the radiation is received in a way that is difficult to predict. The making of model antennae with a smooth exterior might help to clear up the role this morphological trait imparts on an antenna. It would be interesting to contrast an antenna's properties when it contains a smooth exterior vs. a ridged exterior (Callahan, 1991) such as is found on the body setae of the cat flea larva (Figure 6-10). What this difference would entail is out of the scope of this dissertation, but because there is a morphological difference, no matter how slight, a functional difference is expected to exist.

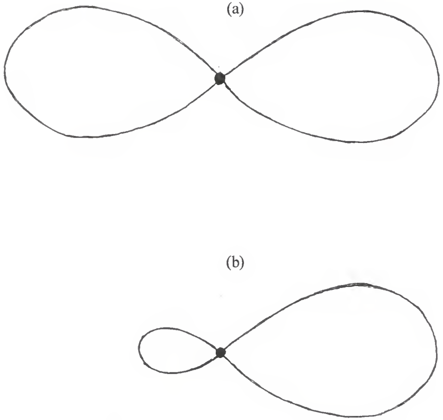


Figure 7-1. Diagrammatic radiation lobe patterns for two hypothetical antennae exhibiting a poor front-to-back ratio (a); and a relatively good front-to-back ratio (b).

Body Setae

The body setae on cat flea larvae are found on all flea larvae of the world (Pilgrim, pers. comm.[1]), but their functional role is unknown. There must be a reason for their existence since unnecessary structures disappear over time in organisms that have no need of them. For example, male adult fleas have antennal suckers which serve to grasp the female during copulation. These structures have reportedly been lost in *Spilopsyllus cuniculi* and the totally unrelated *Chimaeropsylla potis*, both of whom are sessile or semi-sessile species (Rothschild, 1975). Furthermore, fleas apparently had wings at one point in their early history, but now lack them completely (Chapman, 1982). If wings were absolutely necessary for existence they would have been retained. This tells me that because setae have remained in the genetic line for so long, they must be assumed as having an important function, if not more than one function.

Setae as a defensive structure seem to me an unlikely possibility. I have observed fire ants carting my flea larvae away as fast as they could. The ants appeared to have no difficulty in handling their prey. The relatively thin morphology of the seta sacrifices the hardiness of the spine which although firmly attached, is easily bent, and therefore argues against a defensive function, at least in whole. Additionally, cat flea larvae often form aggregations and in the process of climbing over one another for sometimes up to an hour, were never observed to puncture their neighbors, even though cat flea larvae are extremely soft-bodied. When it appeared that some had indeed done so, close observation revealed that instead several setae from each larva had simply interlocked thus forming a temporary union between the two fleas. The flea larvae were observed to quickly separate themselves from one another as soon as they were able.

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[1] R.L.C. Pilgrim, Emeritus Professor of Zoology, University of Canterbury, New Zealand, correspondence dated August 28, 1995.

House fly larvae are heavily preyed upon and parasitized by a host of predators and parasites (Rutz and Axtell, 1981; Geden and Axtell, 1988; Geden et al., 1988) which might have a hard time attacking a fly if it had some external defensive structure. Defense from predators might seem especially important to an insect that is attacked by no less than 7 pupal parasitoids which were solely collected from a poultry manure environment (Rutz and Axtell, 1981). Another study found over 120 beetles in poultry manure, many of which were observed feeding upon the housefly larvae (Pfeiffer and Axtell, 1980). Heavy predation upon houseflies brings up the question as to why houseflies have developed no obvious external defensive structures. Indeed, they might need defensive spines more than the fleas.

The body setae found on cat flea larvae may resonate to sound vibrations such as do the long sensilla found on *Aedes aegypti* (Callahan, 1970) and the long setae on *Barathra brassicae* (Tautz, 1978). Of course, it is not impossible for them to possess a dual function as EM receivers. The similarity between the detection of these differing modalities (one is a sinusoidal wave while the other is a transverse wave) is that both types of antennae have the reception of their respective wavelengths dependent upon the antenna's length. The length of an antenna for either a sound wave or an electromagnetic wave is critical. All antennae designed for receiving EM frequencies are necessarily restricted in their morphology, especially length (Kiely, 1953) and the long setae on *B. brassicae* are restricted to the detection of certain sound frequencies as well (Markl and Tautz, 1975). The body setae differ from the antennae proper in the frequencies that they might receive, which must be the case since a small change in morphology will cause a concomitant change in the properties of that antenna.

Additionally, the body setae are arranged in rows and radial arrays which means they if they are receiving EM frequencies, they would be able to do so with the added benefit of processing the incoming frequencies as an array, and not necessarily as an individual element. An array generally requires systematic placement of elements. This condition has been met by the flea larvae (Figure 6-9). Processing of this information must begin at the surface of the insect and not at the level of the nerve endings, which is how most postulated mechanisms of insect antennal and sensilla communication usually, and disappointingly, begins. There are over 400 different sensilla shapes that exist on insects (Callahan, 1975a) and nine different sensilla types on flea larvae alone (Pilgrim, 1991a) and yet they have been totally ignored when it comes to analyzing insect sensory perception. Since insect sensilla have been convincingly linked with sensory perception, reason dictates that the various shapes of these sensilla must be expected to hold some vital part in the sensory process.

Because not all sensilla on a particular insect are all of the same length, one should expect differences in the responses of different sensilla. A particular sensillum should be consistent in its response, but differ from its neighbors, or sensilla on different individuals. Considerable variation in the relative responsiveness of lactic acid-excited neurons from different sensilla were found by Davis (1988). However, a single sensillum was relatively constant in its response. The differences in responses of the sensilla on a given insect should allow for discrimination of several intensities of lactic acid. This would be extremely useful to the insect. Sensory processing could first occur at the cuticular surface before the nerves even received a stimulus to initiate an action potential.

If the array is electronically fed by the electrical potential existing between the insect's environment and the internal milieu, then a small change in physiology can alter the perception of these electromagnetic frequencies. Man-made arrays have already taken advantage of this property by the use of electronically controlled phase shifters on each element of a "phased" array, which allows the beam-pointing direction of an array antenna to be varied rapidly and without any mechanical movement of the antenna (Smith, 1988). This is in contrast to a fixed beam antenna which needs to move, usually revolve, in order to scan the environment. Is the insect biologically able to adjust the properties of its own array by physiologically altering the electrical properties of the antennal array? The insect may not be able to instantaneously change its phase shifters, but the theoretical possibility exists that they can accomplish this, even if it takes several minutes. As I have shown in Chapter 6, cat flea larvae can locate me within 10-30 minutes. If I shake them up after they have already "tuned in" to me, they can relocate me, by moving over to my side of the petri dish, within 2-6 minutes under controlled conditions (see Chapter 5 and Figure 6-38).

The likelihood that the body setae are acting as dielectric waveguides would make no difference whether the electromagnetic frequency received originated from a relatively distant source across atmospheric space, or whether it originated from a group of molecules in close proximity to the setae, that is, if they are not already attracted to the setae due to the electret properties (Callahan, 1975). Infrared radiation from molecules in a sufficiently small space-time region has coherence (Mehta and Wolf, 1964). The adhesion, or adsorption of molecules upon a spine would certainly qualify as being in a sufficiently small space-time region.

The large number of closely spaced body setae may also have a role in amplifying an incoming electromagnetic signal. Information theory indicates the possibility of "spatial summation" of EM information signals received simultaneously by "n" elements and of temporal summation of signals repeated "n" times (Presman, 1970). The total signal-to-noise ratio would be increased by a factor of the square root of "n". Hence, if "n" were sufficiently large, the reception of information with a signal intensity below the noise level is certainly possible.

Antennal elements in close electronic proximity to one another may "couple" which means the radiation lobes would overlap. Two rows of bristles are found on the head of the rat flea, *Nosopsyllus fasciatus* (Sharif, 1937). Within these two rows, six to eight bristles are arranged in two's (dorsal, ventral, and lateral pairs). Rows of bristles were also described on the labrum and maxillae and all the bristles face in the same direction (Sharif, 1937). Elbel (1952) observed "...most of the setae, even on the head, are arranged in well-defined transverse rows, and in all the species thus far studied these rows are usually distinct, even when they occupy slightly different positions." Differently facing hairs would not form an effective receiving array, so the regularity of these bristles argues against random chance and points toward some function. The processing capabilities of arrays, including the ability to directionalize a signal, are important advances that may aid the insect immeasurably in responding to its environment.

The fact that body setae on all cat flea larvae increase in length as they proceed posteriorly and that the segments elongate posteriorly as well, suggests some log periodic arrangement tuned to a narrow range of frequencies. The whole body would then be acting as an antenna, with the individual elements consisting of the body setae themselves. Man-made log-periodic antennae (Figure 2-4) generally have shorter and shorter elements that are spaced closer and closer together. The existence of the same situation on flea larvae suggests a similar system working, in this case, for an organism.

Scattering

Another piece of evidence pointing to the possibility that the body setae are EM receivers can be found in the cuticle immediately surrounding the setal base. Instead of the scale-like cuticle which covers most of the body, a smooth surface roughly circular in shape occurs with the seta located at its center. Smooth cuticle, especially with a waxy coating, is highly reflective of electromagnetic radiation (Callahan, 1990). Setae are said to have supporting plates (Pilgrim, 1992) which is exactly what they seem to be from a certain distance. But in the case of the cat flea, the scanning electron micrographs show this region not as a plate, but simply as the absence of scales in a localized region of the cuticle. This is not a random occurrence, but only occurs around the bases of these body setae. If the body setae are EM receivers, then a reflective cuticle at the base of the antennae will certainly create an interaction between incoming radiation that impinges directly upon the seta, and that same radiation which first strikes the cuticle and reflects off on to the seta. An interaction between the two wavelengths occurs which results in destructive and/or constructive interference depending upon what phase each is in. In the infrared, scattering would be expected to be much less important than in the visible since the wavelengths are longer (Bennett and Mattsson, 1989). Therefore, relative differences in infrared radiation scattering may in fact be an effective way of discriminating between various incoming frequencies. Perceiving this complex interaction occurring at the surface of the flea larva's cuticle may be of use to the flea. Body setae and articulations of the cuticle may seem insignificant but as Ron Pilgrim writes "I agree with Traub (1972) that '...we are now learning to appreciate that so many seemingly insignificant structural modifications of [adult] fleas do have meaning or function...'". I agree wholeheartedly with both in that it not only applies to adult fleas, as the quote is intended, but to flea larvae as well.

The perception of these EM frequencies is traditionally determined in entomology by the use of electrophysiological apparatus. What this involves is sticking a pin into the base of the spine, puncturing the innervating nerve with the tip of this pin, and recording any action potentials which may be elicited. Dielectric antennae should never be punctured as such since a break in the continuity of the antenna would create an electrical leak. The system one would be attempting to record would now be compromised by the very procedure used to test it. Additionally, just because an electrophysiological response is obtained, let us say with heat or pressure, does not mean that this is what the receptor is tuned to. Rubbing your eye with your eyelid closed causes apparent blotches of light to appear in that eye. This perception of light is not coming from any light source, but rather the nerves firing action potentials in response to an unnatural pressure stimulus.

Molecular Emissions

The possibility that carbon dioxide (CO_2) was mediating the orientation response is a subject worthy of discussion. Adult fleas, like other hematophagous arthropods, locate their hosts by kairomones emanating from the host (Hinkle et al., 1991). These include carbon dioxide and other volatiles (Smith et al., 1970; Vale, 1980; 1984). There are arguments both for and against this molecule's involvement in cat flea orientation. Two pilot experiments argue against it. Dry ice (frozen CO_2) was unable to elicit a positive orientational response nor was I able to do so when I continually "breathed" upon the petri dish for over 45 minutes. However, the height experiments showed that the fleas' response became progressively worse as the petri dish's distance above my head increased. Since CO_2 is heavier than air, the likelihood that flea larvae would be able to detect CO_2 emanating from my breath would also decrease with increasing heights.

It might be that CO_2 is involved in the orientation response, but it may be only one of many factors that the fleas consider. The flea larvae may also be orienting to some other molecule emanating from my body that is also heavier than air, but because breathing upon the flea larvae did not elicit an orientation response the molecule may not come from human exhalations.

There is the possibility that radiation emitted from molecules may be detected by the body setae directly.

Fleas and Electromagnetism

The effects of magnetism or electromagnetism on fleas have been demonstrated in several experiments. No experiments were conducted testing the effects of a pure electric field via magnetic shielding, however, a positive result seems to me, inevitable. It should be made clear that the behavior of fleas around magnets or an electromagnetic field is only known insofar as my experiments have shown. Flea larvae are sensitive to magnets at the intensity they were subjected to (up to 2500 Gauss), under the time course studied (only one hour), while comparing its behavior to a human stimulus. Different experimental set-ups, might yield different results. An electromagnetic influence was shown for flea larvae only at the field tested (4.1×10^{-3} V/m) but no attempt was made to find the minimum electric (electromagnetic) field that would influence the flea larvae.

No physiological parameters were investigated in this study, which means no direct knowledge was obtained of how electromagnetic fields might affect the fleas physiologically. As I have clearly stated in Chapter 2, reductionist science might have led to erroneous results since a negative result while testing a single physiological parameter might have caused me to conclude that no effect of magnetism on the fleas was observed. However, approaching this from a behavioral level, has enabled me to make the claim that the fleas are indeed influenced by electromagnetic energy including its magnetic component, but because of the behavioral approach I may only speculate at this time how the fleas might be doing this.

Since electromagnetic energy is detected by tuned structures which may take an infinite variety of shapes (antennae) my speculations that the flea detects these frequencies via the antennae proper and/or the body setae is entirely possible. As direct evidence is difficult to obtain, I feel that I should continue to provide indirect suggesting arguments which, by their cumulative effects, would lead, in the course of time, to a definitive adoption.

Cat flea larvae have a log-periodic antennal arrangement, suggesting that the body acts as an antenna; they have an antenna outfitted with 5 modifiers on only one side, which likely imparts directionality to the antenna; they have an antennal seta with four directors in the shape of spines at the base of this seta; they have a reflective cuticle at each base of a body seta, which is formed by the conspicuous absence of scales; and the cuticle itself is arranged in a beautiful pattern suggestive of a radiative scattering surface. For these reasons, I believe the cat flea larva to be a highly efficient living antenna.

APPENDIX
ADDITIONAL BREAKDOWN DATA

Breakdown data for all experiments whereby data acquisition occurred every 2 minutes is given in this Appendix. Breakdown data by 20 and 30 minute increments are given. All figures are shown first, followed by all tables.

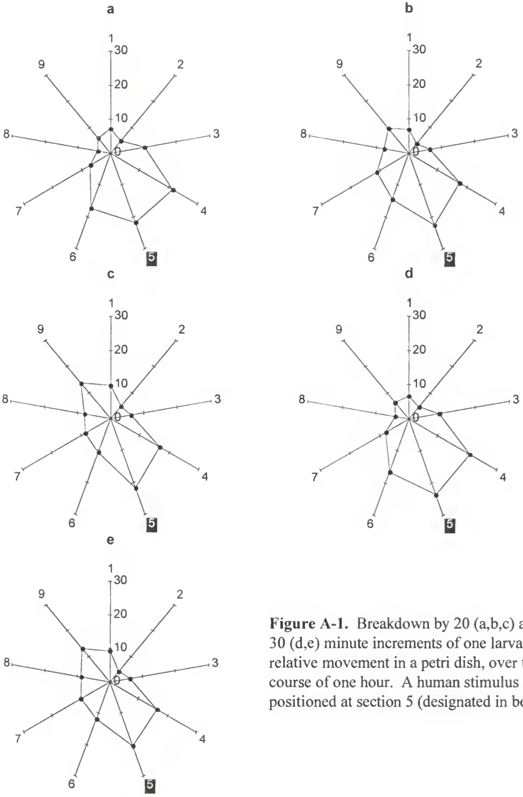


Figure A-1. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour. A human stimulus is positioned at section 5 (designated in bold).

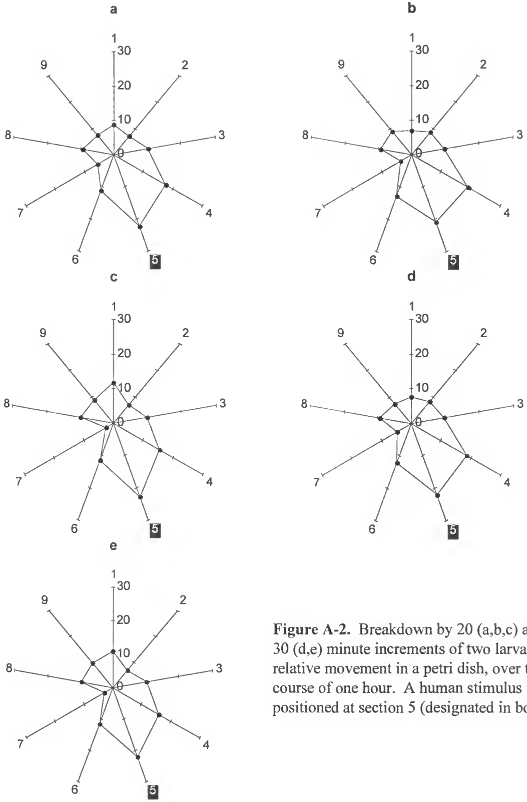


Figure A-2. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of two larvae's relative movement in a petri dish, over the course of one hour. A human stimulus is positioned at section 5 (designated in bold).

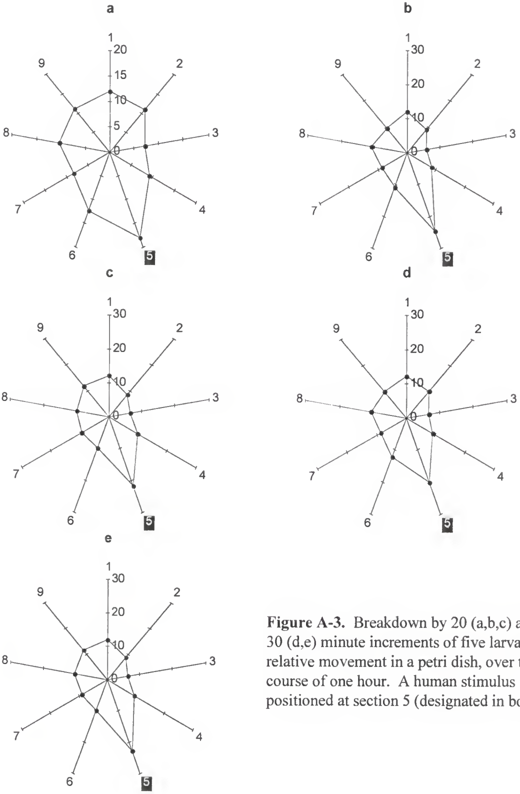


Figure A-3. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of five larvae's relative movement in a petri dish, over the course of one hour. A human stimulus is positioned at section 5 (designated in bold).

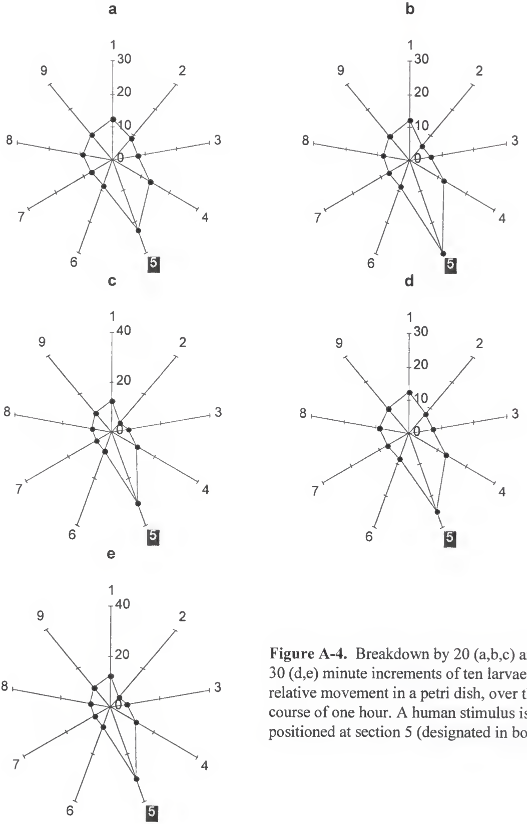


Figure A-4. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of ten larvae's relative movement in a petri dish, over the course of one hour. A human stimulus is positioned at section 5 (designated in bold).

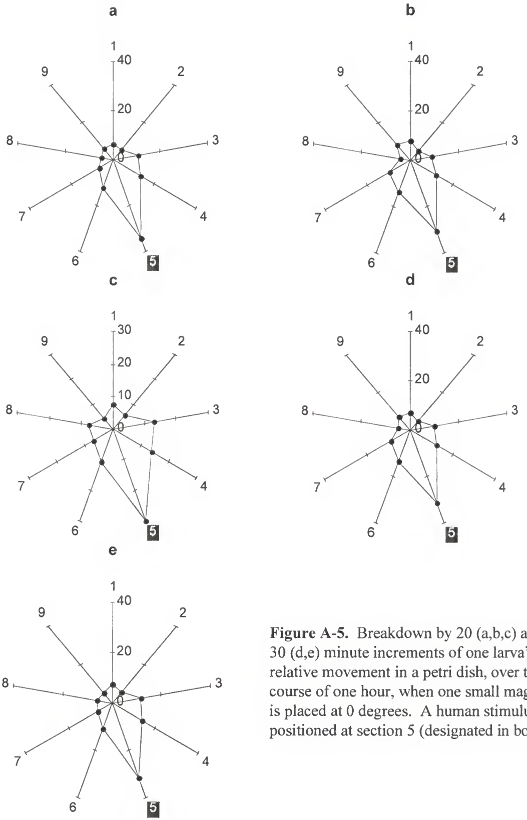
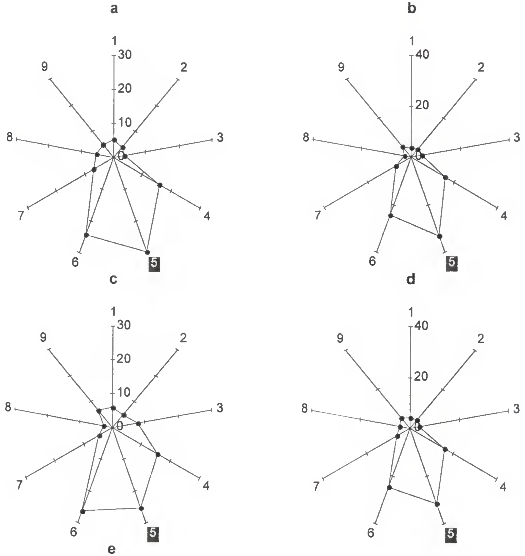


Figure A-5. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one small magnet is placed at 0 degrees. A human stimulus is positioned at section 5 (designated in bold).



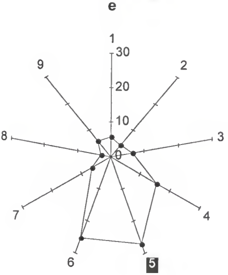


Figure A-6. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one small magnet is placed at 90 degrees. A human stimulus is positioned at section 5 (designated in bold).

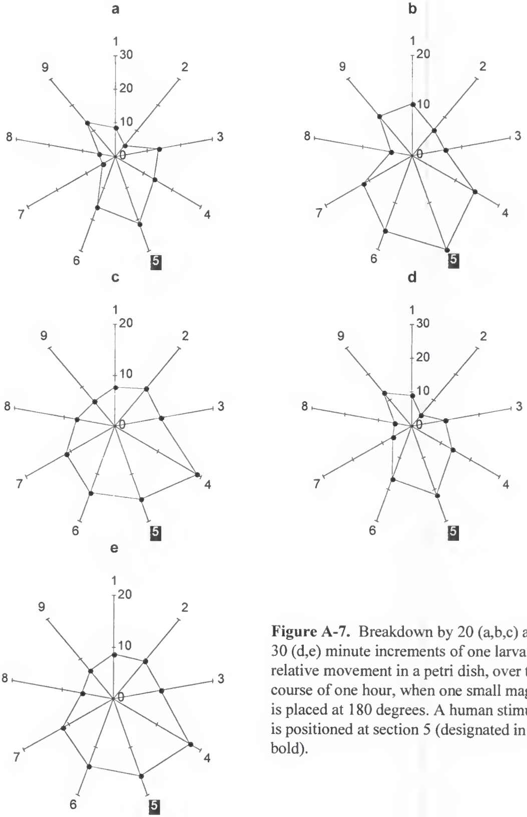


Figure A-7. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one small magnet is placed at 180 degrees. A human stimulus is positioned at section 5 (designated in bold).

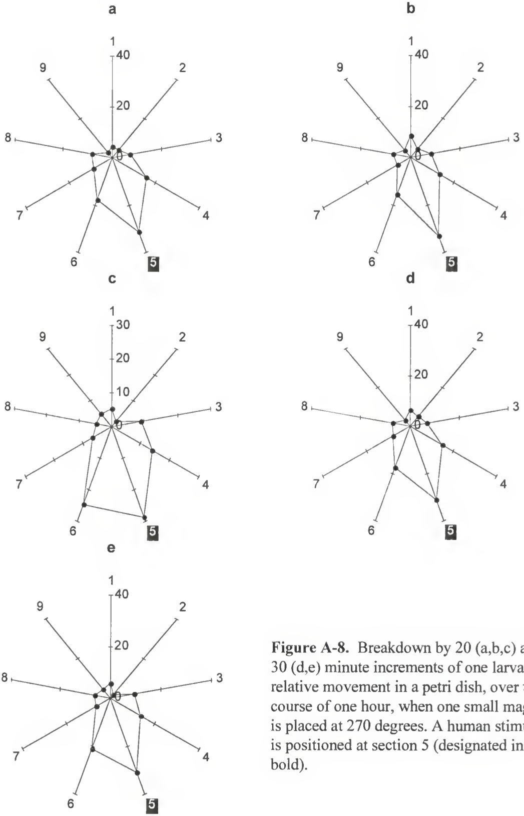
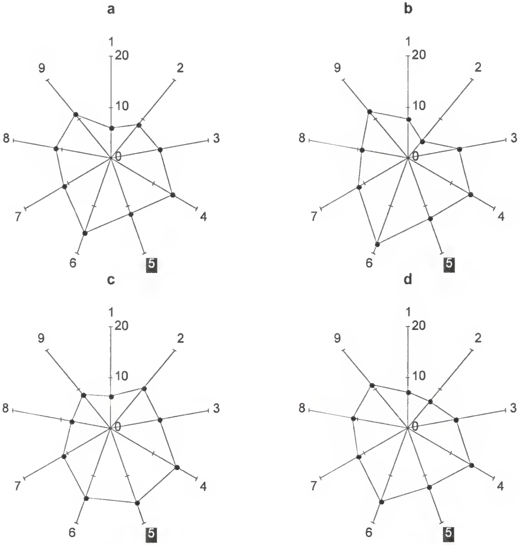


Figure A-8. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one small magnet is placed at 270 degrees. A human stimulus is positioned at section 5 (designated in bold).



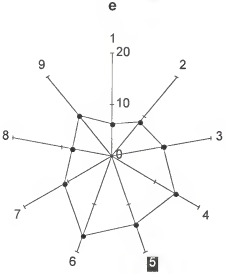


Figure A-9. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one small magnet is placed on the top/center of that petri dish. A human stimulus is positioned at section 5 (designated in bold).

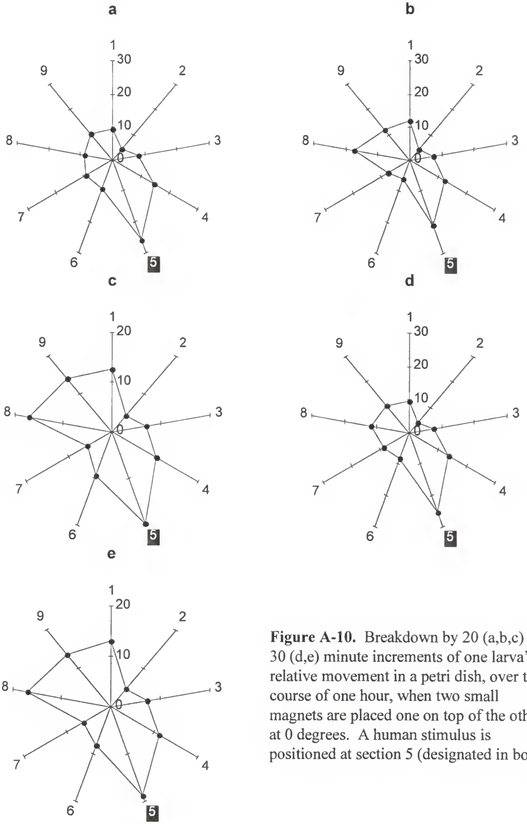


Figure A-10. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when two small magnets are placed one on top of the other at 0 degrees. A human stimulus is positioned at section 5 (designated in bold).

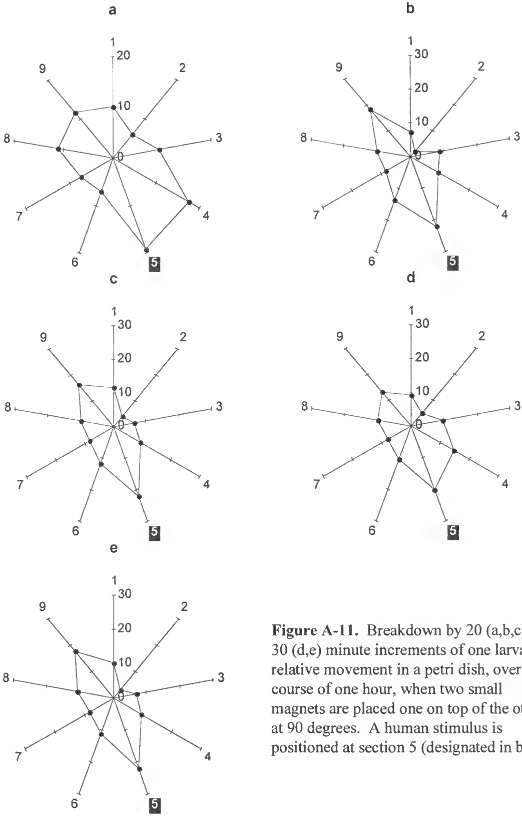
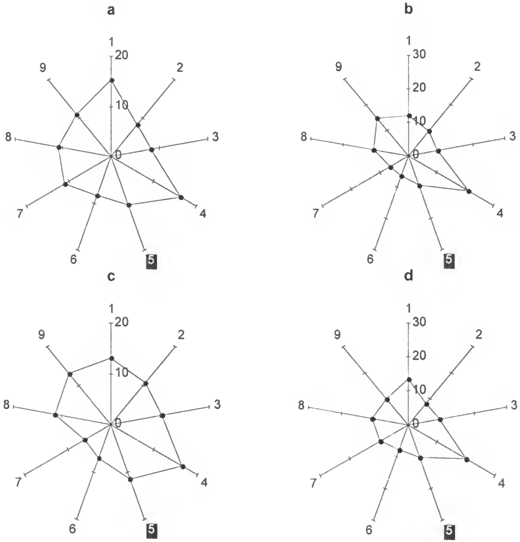


Figure A-11. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when two small magnets are placed one on top of the other at 90 degrees. A human stimulus is positioned at section 5 (designated in bold).



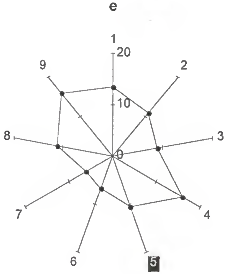


Figure A-12. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when two small magnets are placed one on top of the other at 180 degrees. A human stimulus is positioned at section 5 (designated in bold).

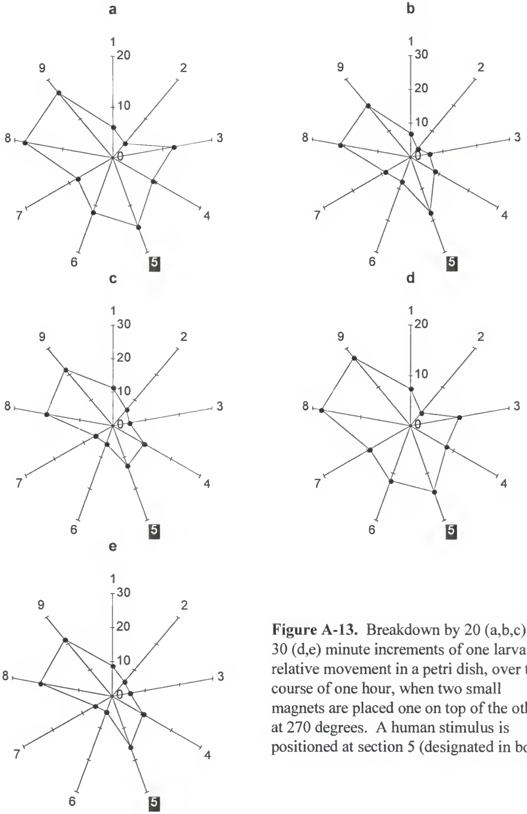
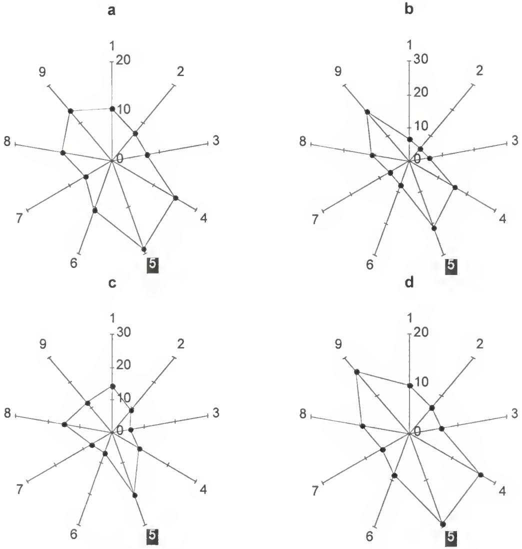


Figure A-13. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when two small magnets are placed one on top of the other at 270 degrees. A human stimulus is positioned at section 5 (designated in bold).



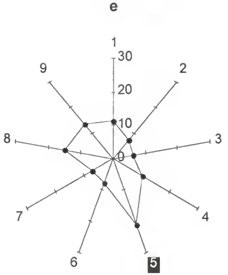


Figure A-14. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when two small magnets are placed one on top of the other on the top/center of that petri dish. A human stimulus is positioned at section 5 (designated in bold).

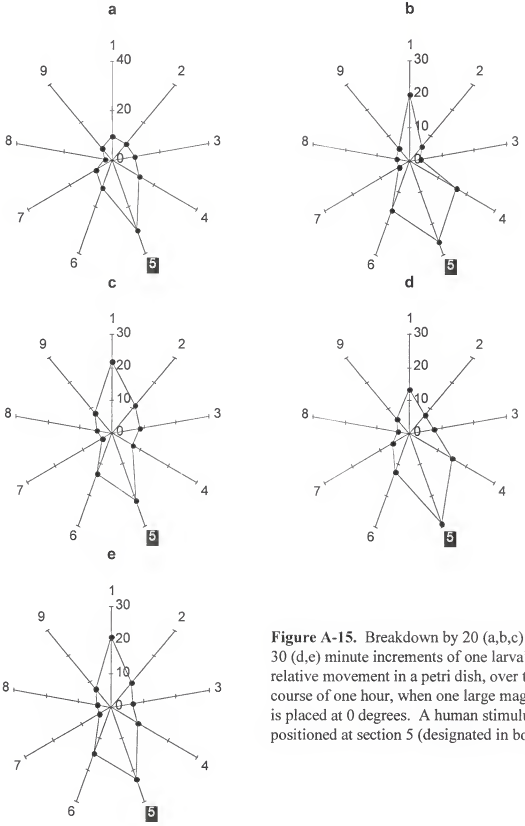


Figure A-15. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one large magnet is placed at 0 degrees. A human stimulus is positioned at section 5 (designated in bold).

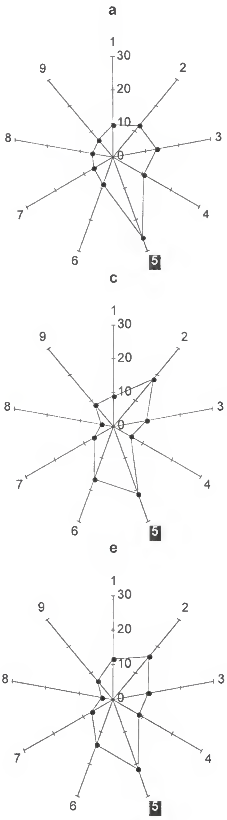


Figure A16. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one large magnet is placed at 90 degrees. A human stimulus is positioned at section 5 (designated in bold).

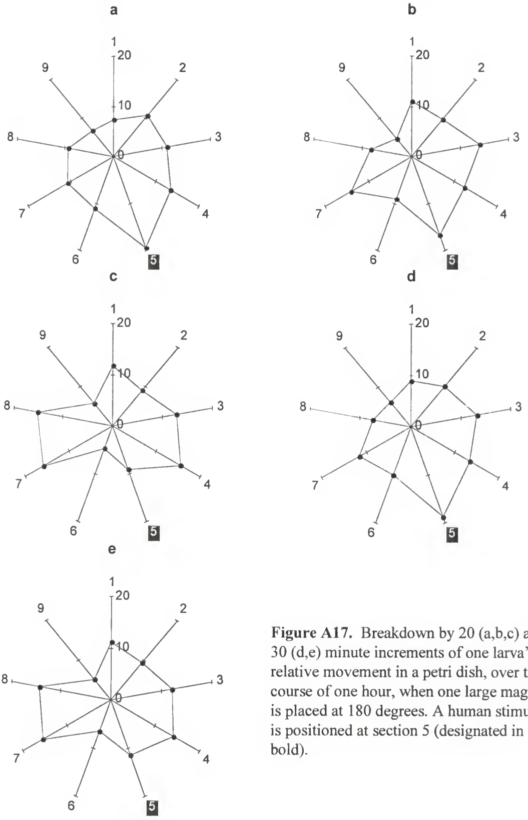


Figure A17. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one large magnet is placed at 180 degrees. A human stimulus is positioned at section 5 (designated in bold).

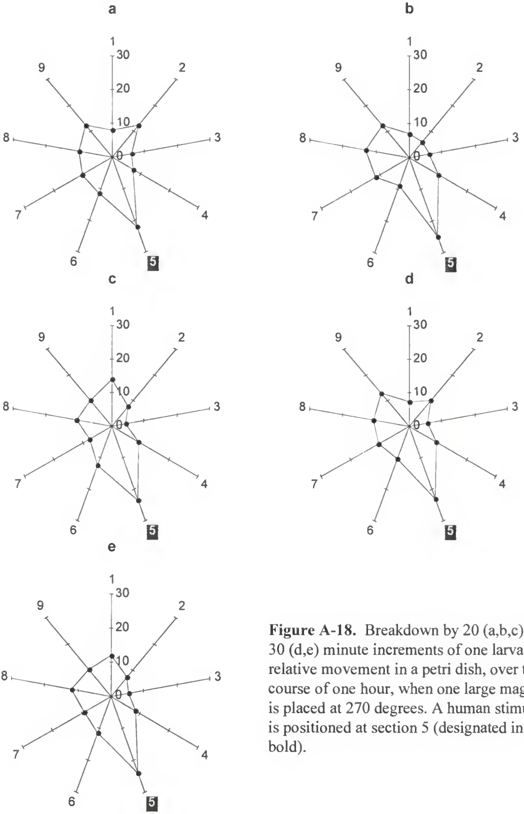
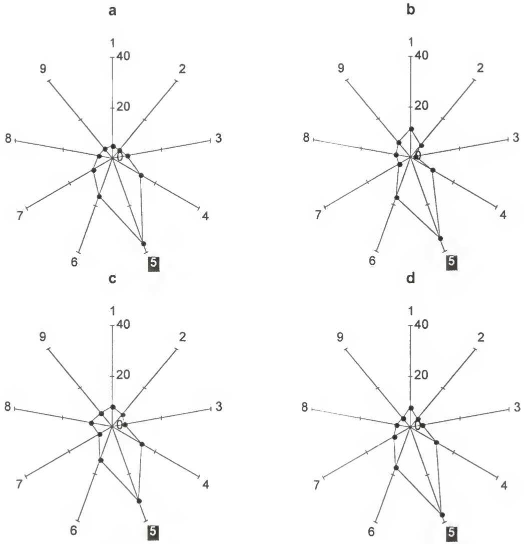


Figure A-18. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when one large magnet is placed at 270 degrees. A human stimulus is positioned at section 5 (designated in bold).



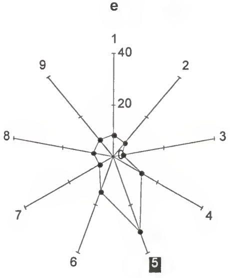


Figure A-19. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when four small, adjacent magnets are placed underneath the petri dish. A human stimulus is positioned at section 5 (designated in bold).

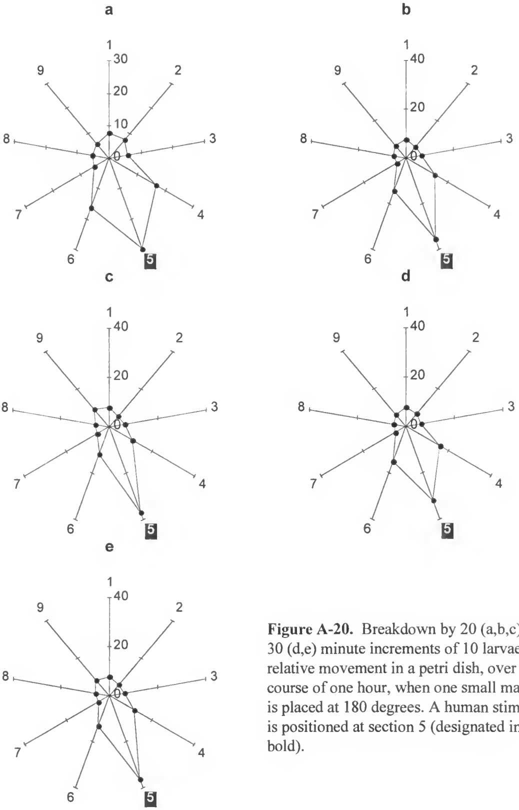
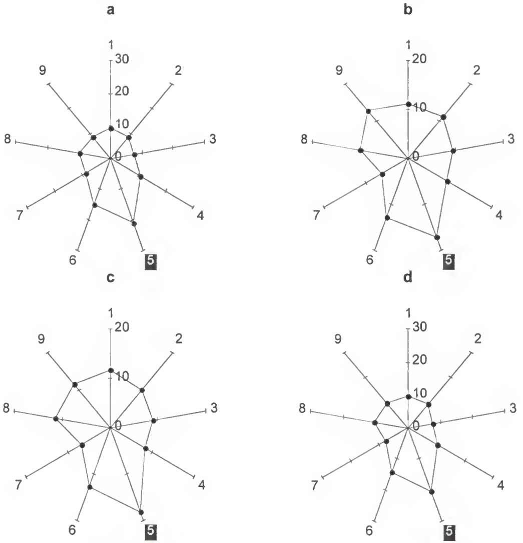


Figure A-20. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when one small magnet is placed at 180 degrees. A human stimulus is positioned at section 5 (designated in bold).



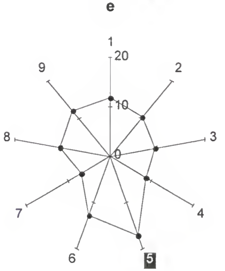


Figure A-21. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when two small magnets are placed one on top of the other at 180 degrees. A human stimulus is positioned at Section 5 (designated in bold).

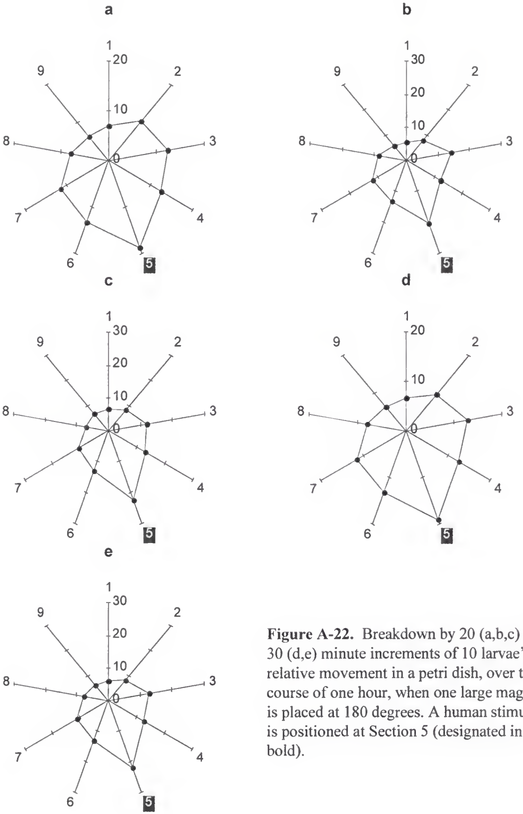


Figure A-22. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when one large magnet is placed at 180 degrees. A human stimulus is positioned at Section 5 (designated in bold).

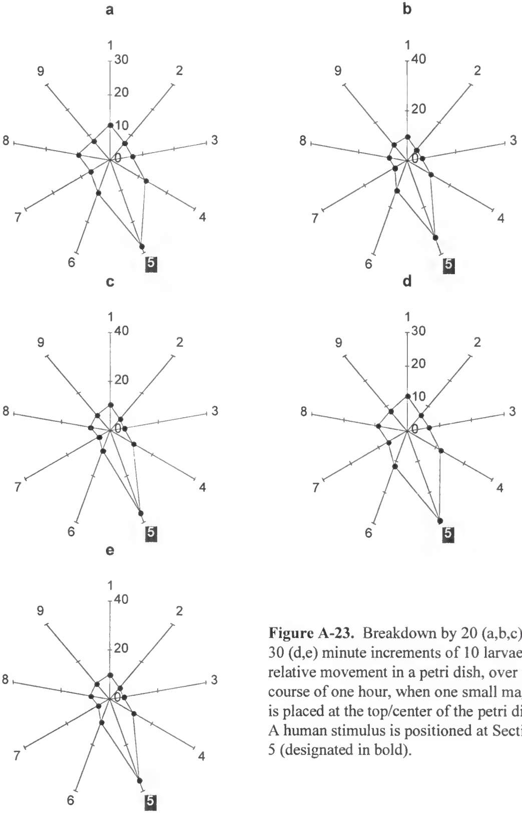
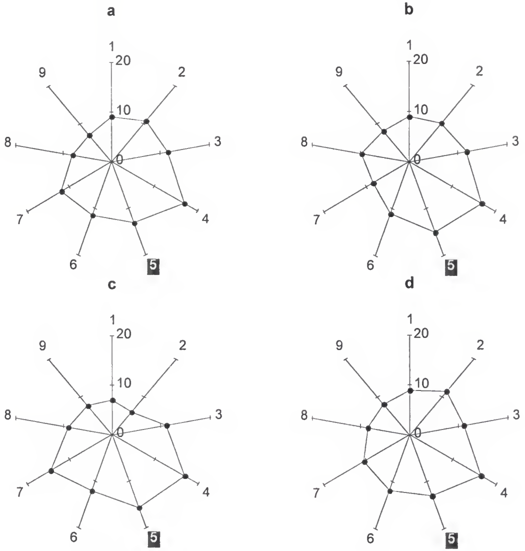


Figure A-23. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of 10 larvae's relative movement in a petri dish, over the course of one hour, when one small magnet is placed at the top/center of the petri dish. A human stimulus is positioned at Section 5 (designated in bold).



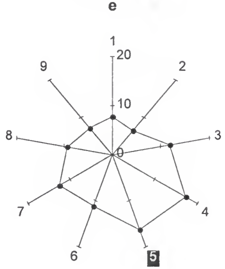


Figure A-24. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan is turned off and a glass cover is placed over the experiment. A human stimulus is positioned at section 5 (designated in bold).

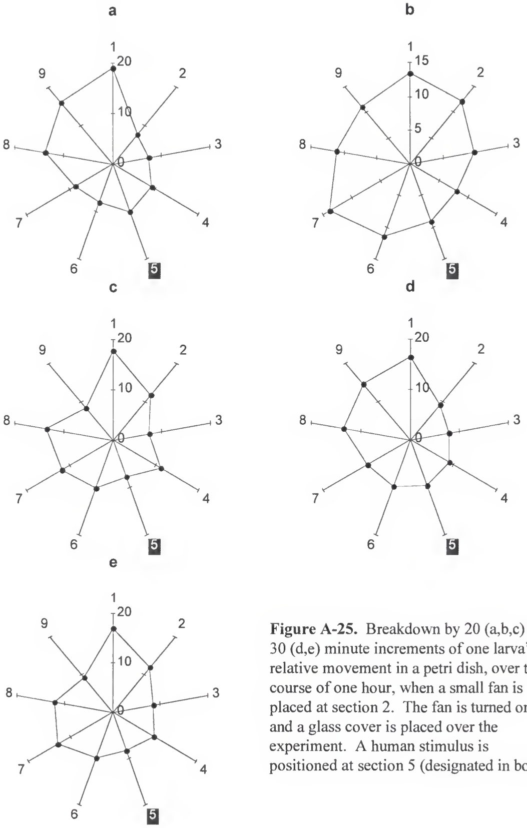
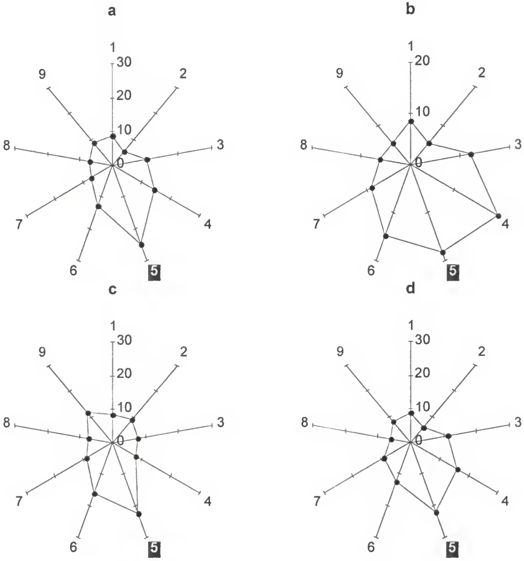


Figure A-25. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan is turned on and a glass cover is placed over the experiment. A human stimulus is positioned at section 5 (designated in bold).



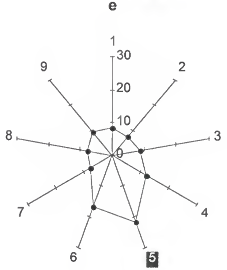
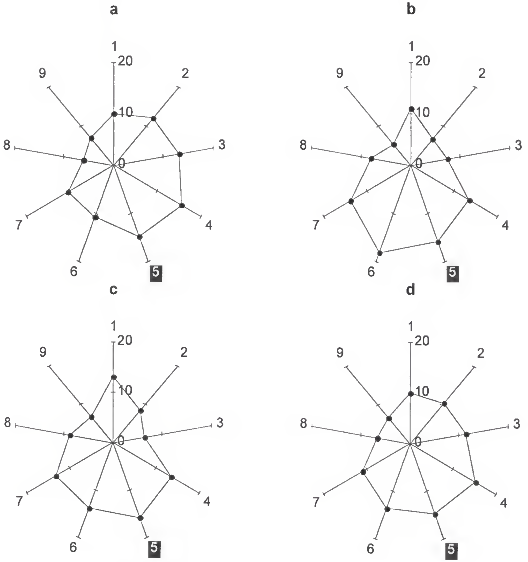


Figure A-26. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan is turned off, and there is no cover over the experiment. A human stimulus is positioned at section 5 (designated in bold).



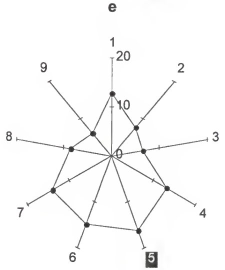


Figure A-27. Breakdown by 20 (a,b,c) and 30 (d,e) minute increments of one larva's relative movement in a petri dish, over the course of one hour, when a small fan is placed at section 2. The fan is turned on, but no glass covers the experiment. A human stimulus is positioned at section 5 (designated in bold).

Table A-1. Number Experiments. Breakdown analysis into 20 and 30 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiment	**0-20**	**21-40**	**41-60**	**0-30**	**31-60**
1 larva	37.37	26.70	21.29	38.84	18.32
2 larvae	21.49	22.55	23.16	23.11	21.06
5 larvae	**6.89**	20.82	**13.46**	10.36	15.84
10 larvae	16.63	38.79	42.27	22.65	41.40

Table A-2. Number Experiments. Breakdown analysis into 20 and 30 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Experiment	**0-20**	**21-40**	**41-60**	**0-30**	**31-60**
1 larva	12.70	14.16	20.36	15.07	14.36
2 larvae	20.46	18.78	25.89	20.13	22.57
5 larvae	12.81	39.56	25.59	19.38	31.02
10 larvae	29.02	60.97	65.72	38.27	64.47

Table A-3. Magnet Experiments. Breakdown analysis into 20 and 30 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiment	**Location**	**0-20**	**21-40**	**41-60**	**0-30**	**31-60**
1 magnet	**0**	61.68	45.28	43.66	48.72	49.87
	90	69.76	85.34	59.64	79.32	61.94
	180	25.20	18.00	**12.62**	23.88	**11.21**
	270	60.16	59.66	64.78	56.03	63.57
	T/C	**5.84**	**11.04**	**8.24**	**6.28**	**8.46**
2 magnets	**0**	27.54	21.40	19.34	26.58	17.27
	90	**15.05**	26.51	21.02	**14.10**	23.18
	180	**6.20**	**15.30**	**7.18**	**10.07**	**9.17**
	270	16.69	32.36	28.65	16.95	33.79
	T/C	**12.12**	28.20	16.34	17.74	16.59
Lg. magnet	**0**	42.39	52.20	32.68	43.01	34.91
	90	26.00	25.90	27.20	25.38	22.03
	180	**10.04**	**9.50**	**12.60**	**9.96**	**8.97**
	270	15.72	24.34	21.29	17.58	20.18
4 adj. magn.	**Under**	74.50	67.72	48.84	78.11	47.96

Table A-4. Magnet Experiments. Breakdown analysis into 20 and 30 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Experiment	Location	0-20	21-40	41-60	0-30	31-60
1 magnet	**0**	61.31	44.48	44.39	47.32	52.14
	90	39.11	46.25	30.78	44.59	31.14
	180	14.66	9.37	5.83	13.99	3.94
	270	36.23	51.97	32.77	38.70	36.98
	T/C	3.00	4.70	2.15	2.48	2.54
2 magnets	**0**	33.91	31.22	21.54	37.53	19.61
	90	22.95	21.90	25.92	14.10	25.64
	180	9.90	34.27	14.24	21.60	14.18
	270	4.84	19.17	11.33	4.64	21.86
	T/C	14.36	28.57	31.37	20.55	29.21
Lg. magnet	**0**	45.48	34.51	33.19	40.85	30.96
	90	40.32	25.97	31.46	38.08	22.07
	180	9.25	7.09	19.70	8.71	9.56
	270	31.03	39.69	33.26	31.21	36.10
4 adj. magn.	**Under**	63.74	78.56	52.59	73.20	54.99

Table A-5. Magnet 10 Experiments. Breakdown analysis into 20 and 30 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Experiments	0-20	21-40	41-60	0-30	31-60
1 magnet	50.31	69.52	72.36	56.24	70.02
2 magnets	**13.65**	**6.67**	**7.67**	**11.51**	**6.17**
Lg. magnet	**10.48**	15.96	18.13	**11.37**	17.78
1 magnet t/c	31.45	51.49	65.40	35.72	62.36

Table A-6. Magnet 10 Experiments. Breakdown analysis into 20 and 30 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Experiments	0-20	21-40	41-60	0-30	31-60
1 magnet	38.86	70.03	92.30	48.69	82.59
2 magnets	16.43	11.21	15.03	16.70	11.63
Lg. magnet	5.67	8.62	13.76	6.20	12.26
1 magnet t/c	44.47	67.07	98.85	49.61	89.24

Table A-7. Fan 2 Experiments. Breakdown analysis into 20 and 30 minute blocks. Chi-square values testing goodness of fit to a circle are shown. Values in bold indicate a goodness of fit to a circle at p= 0.05.

Cover	**Fan**	**0-20**	**21-40**	**41-60**	**0-30**	**31-60**
On	**Off**	**6.09**	**6.52**	**11.14**	**4.77**	**10.61**
On	**On**	**12.78**	**2.61**	**7.71**	**6.45**	**5.58**
Off	**Off**	25.12	21.83	18.47	19.57	17.84
Off	**On**	**7.33**	**14.39**	**8.82**	**6.92**	**10.83**

Table A-8. Fan 2 Experiments. Breakdown analysis into 20 and 30 minute blocks. Degree of directivity (D.O.D.) indices for testing level of directivity toward Section 5 are shown.

Cover	**Fan**	**0-20**	**21-40**	**41-60**	**0-30**	**31-60**
On	**Off**	3.84	5.93	3.31	3.32	5.05
On	**On**	0.93	3.19	2.86	0.41	1.78
Off	**Off**	22.55	7.00	26.62	12.90	15.42
Off	**On**	3.52	6.08	4.57	1.31	5.07

LIST OF REFERENCES

Abler, R.A. (1969) Magnets in biological research. In: Biological Effects of Magnetic Fields, Vol. 2. Plenum Press, New York. pp. 1-28.

Adam, G. and M. Delbrück (1968) Reduction of dimensionality in biological diffusion processes. In: Structural Chemistry and Molecular Biology. A. Rich and N. Davidson (eds.) Freeman, San Francisco. pp. 198-215.

Agee, H.R., E.R. Mitchell, and R.V. Flanders (1990) Spectral sensitivity of the compound eye of *Coccinella septempunctata* (Coleoptera: Coccinellidae). Ann. Entomol. Soc. Am. 83(4):817-819.

Aladzhalova, N.A. (1962) Slow electric processes in the brain. Izd. Akad. Nauk. SSSR, Moscow.

Amin, O.M. (1966) The fleas (Siphonaptera) of Egypt: distribution and seasonal dynamics of fleas infesting dogs in the Nile valley and delta. J. Med. Entomol. 3(3-4):293-298.

Arendse, M.C. (1978) Magnetic field detection is distinct from light detection in the invertebrates *Tenebrio* and *Talitrus*. Nature, 274:358-362.

The ARRL Antenna Book (1974) 13th ed. The American Radio Relay League, Inc. 336 pp.

Athenstaedt, H. and H. Claussen (1981) Evidence for pyroelectric and piezoelectric sensory mechanisms in the insect integument. Biophys. J. 35:365-374.

Baker, V.H., D.E. Wiant, and O. Taboada (1956) Some effects of microwaves of certain insects which infest wheat and flour. J. Econ. Entomol. 49(1):33-37.

Balashov, Y.S. (1984) Interaction between blood-sucking arthropods and their hosts, and its influence on vector potential. Ann. Rev. Entomol. 29:137-156.

Barlow, H.B. (1982) Physiology of the retina. In: The senses. H.B. Barlow and J.D. Mollen (eds.) Cambridge Univ. Press. pp. 102-113.

Barnes, A.M. and F.J. Radovsky (1969) A new *Tunga* (Siphonaptera) from the Nearctic region with description of all stages. J. Med. Entomol. 6:19-36.

Barnes, R.B. (1963) Thermography of the human body. Science, 140:870-877.

Barnothy, M.F. (ed.) (1969) Biological effects of magnetic fields. Plenum Press, New York. 314 pp.

Barrow, W.L. (1936) Transmission of electromagnetic waves in hollow tubes of metal. Proc. IRE 24:1298-1328.

Beament, J.W.L. (1961) Electrical properties of oriented lipid on a biological membrane. Nature, 191:217.

Becker, G. (1963a) Ruheeinstellung nach der Himmelsrichtung, eine Magnetfeld-Orientierung bei Termiten. Naturwissenschaften 50:455.

Becker, G. (1963b) Reaction of insects to magnetic fields. Second Inter. Biomagnet. Symp. p. 19.

Becker, G. (1971) Magnetfeld-Einfluβ auf die Galeriebau-Richtung bei Termiten. Naturwissenschaften, 58:60.

Becker, G. (1976a) Reaction of termites to weak alternating magnetic fields. Naturwissenschaften 63:201-202.

Becker, G. (1976b) Physical, chemical and biological factors influencing the damage of wood and other materials by temites. Proc. 3rd Int. Biodegradation Symp. pp. 259-271.

Becker, G. (1976c) Termiten verständigen sich elektrisch. Umschau, 76:555-565.

Becker, G. (1977a) Communication between termites by biofields. Biol. Cybernetics, 26:41-44.

Becker, G. (1977b) Elektrische Kommunikation bei Termiten. Z. ang. Ent. 82:300-306.

Becker, G. (1977c) Compensation of magnetic and electric effects on termites by other, especially chemical influences. Zool. Jb. Physiol. Bd. 81:353-359.

Becker, G. (1989) Communication between termites by means of biofields and the influence of magnetic and electric fields on termites. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 116-127.

Becker, G. and W. Gerisch (1973) Zusammenhänge zwischen der Frassaktivität von Termiten und solaren Einflüssen. Z. angew. Entomol. 73:365-386.

Becker, G. and W. Gerisch (1977) Korrelation zwischen der Frassaktivität von Termiten und der geomagnetischen Aktivität. Z. ang. Ent. 84:353-388.

Becker, G. and U. Speck (1964) Untersuchungen über die Magnetfeldorientierung von Dipteren. Z. vergl. Physiol. 49:301-340.

Becker, R.O. (1969) The effect of magnetic fields upon the central nervous system. In: Biological Effects of Magnetic Fields, Vol. 2. M.F. Barnothy (ed.) Plenum Press, New York. pp. 207-214.

Bennett, J.M. and L. Mattsson (1989) Introduction to surface roughness and scattering. Optical Society of America, Washington, D.C. 112 pp.

Bernhard, A.H. and W.H. Miller (1962) A corneal nipple pattern in insect compound eyes. Acta physiol. scand. 56:385-386.

Bernhard, C.G., W.H. Miller, and A.R. Møller (1965) The insect corneal nipple array. Acta Physiol. Scand. Vol. 63, Suppl. 243. 79 pp.

Bhatnagar, C.S. (1964) The magneto-electret. Indian J. Pure Appl. Phys. 2:331.

Blackman, C.F. (1994) Effect of electrical and magnetic fields on the nervous ststem. In: The Vulnerable Brain and Environmental Risks Vol. 3: Toxins in Air and Water. R.L Isacson and K. Jensen (eds.). Plenum Press, New York. pp. 341-355.

Blackman, C.F. and B. Most (1993) A scheme for incorporating DC magnetic fields into epidemiological studies of EMF exposure. Bioelectromagnetics 14:413-431.

Blakemore, R. (1975) Magnetotactic bacteria. Science, 190:377-379.

Boo, K.S. and A.G. Richards (1975) Fine structure of the scolopidia in the Johnston's organ of male *Aedes aegypti*. Int. J. Insect Morphol. & Embryol. 4:**???.**

Breithaupt, H. (1989) Biological rhythms and communication. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 18-41.

Brown, F.A.. (1963) An orientational response to weak gamma radiation. Biol. Bull. 125:206-225.

Brown, E.A. and E.A. Cameron (1977) Studies on the compound eye of *Lymantria dispar* (Lepidoptera: Lymantriidae) males and behavioral implications. Can. Entomol. 109:255-260.

Bruce, W.N. (1948) Studies on the biological requirement of the cat flea. Ann. Entomol. Soc. Amer. 41:346-352.

Bruce, W.A. (1971) Perception of infrared radiation by the spiny rat mite, *Laelaps echidnina* (Acari: Laelapidae). Ann. Entomol. Soc. Am. 64:925-931.

Burgess, L. (1959) Probing behaviour of *Aedes aegypti* (L.) in response to heat and moisture. Nature, 184:1968-1969.

Burns, E.C. and D. Melancon (1977) Effect of imported fire ant (Hymenoptera: Formicidae) invasion on lone star tick (Acarina: Ixodidae) populations. J. Med. Entomol. 14:247-249.

Bishopp, F.C. (1915) Fleas. U.S.D.A. Bull. #248. 31 pp.

Callahan, P.S. (1957) Oviposition response of the imago of the corn earworm *Heliothis zea* (Boddie), to various wavelengths of light. Ann. Entomol. Soc. Amer. 50(5):444-452.

Callahan, P.S. (1965a) Intermediate and far infrared sensing of nocturnal insects. Part I. Evidences for a far infrared (FIR) electromagnetic theory of communication and sensing in moths and its relationship to the limiting biosphere of the corn earworm, *Heliothis zea*. Ann. Entomol. Soc. Am. 58:727-745.

Callahan, P.S. (1965b) Intermediate and far infrared sensing of nocturnal insects. Part II. The compound eye of the corn earworm, *Heliothis zea*, and other moths as a mosaic optic-electromagnetic thermal radiometer. Ann. Entomol. Soc. Am. 58:746-756.

Callahan, P.S. (1965c) Far infrared emission and detection by night flying moths. Nature, 207:1172-1173.

Callahan, P.S. (1965d) An infrared electromagnetic theory of diapause inducement and control in insects. Ann. Entomol. Soc. Am. 58:561-564.

Callahan, P.S. (1966) Infrared stimulation of nocturnal moths. J. Ga. Ent. Soc. 1:6-14.

Callahan, P.S. (1967) Insect molecular bioelectronics: a theoretical and experimental study of insect sensillae as tubular waveguides, with particular emphasis on their dielectric and thermoelectret properties. Misc. Public. Entom. Soc. Amer. 5(7):315-347.

Callahan, P.S. (1968) A high frequency dielectric waveguide on the antennae of night-flying moths (Saturnidae). J. Appl. Optics 7:1425-1430.

Callahan, P.S. (1969) The radiation environment and its relationship to possible methods of environmental control of insects. Proc. Tall Timbers Conf. Ecol. Anim. Control by Habitat Manag. February 27-28, 1969. pp. 85-108.

Callahan, P.S. (1971) Insect Behavior. Four Winds Press, New York. 155 pp.

Callahan, P.S. (1973) Studies on the shootborer *Hypsipyla grandella* (Zellar) (Lep., Pyralidae). XIX. The antenna of insects as an electromagnetic sensory organ. Turrialba 23(3):263-274.

Callahan, P.S. (1975a) Insect antennae with special reference to the mechanism of scent detection and the evolution of the sensilla. Int. J. Insect Physiol. & Embryol. 4(5):381-430.

Callahan, P.S. (1975b) Tuning in to Nature. Devin-Adair Co., Old Greewich, Conn. 240 pp.

Callahan, P.S. (1977a) Solid state organic (pheromone-beeswax) far infrared maser. Appl. Opt. 16(6):1557-1562.

Callahan, P.S. (1977b) Comments on Mark Diesendorf's critique of my review paper. Int. J. Insect Morphol. & Embryol. 6(2):111-122.

Callahan, P.S. (1979) John Tyndall: unifier of 19th century science. Appl. Opt. 18(3):255-258.

Callahan, P.S. (1981) John Tyndall- contributions to the development of infrared and solid state communications. In: John Tyndall, essays on a natural philosopher. W.H. Brock, N.D. McMillan, and R.C. Mollan (eds.). Royal Dublin Society, historical studies in Irish science and technology, no. 3. pp. 129-144.

Callahan, P.S. (1985) Dielectric waveguide modeling at 3.0 cm of the antenna sensilla of the lovebug, *Plecia nearctica* Hardy. Appl. Optics, 24:1094-1097.

Callahan, P.S. (1989) Treating the AIDS virus as an antenna. 21st Century. March-April, 26-31.

Callahan, P.S. (1990) Nonlinear infrared coherent radiation as an energy coupling mechanism in living systems. In: Molecular and biological physics of living systems. R.K. Mishra (ed.) Kluwer Academic Publishers, Netherlands. pp. 239-273.

Callahan, P.S. (1991) Dielectric waveguide (open resonator) models of the corn earworm, sensilla: sensilla relationship to infrared coherent molecular scatter emissions from semiochemicals (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 84(4):361-368.

Callahan, P.S. (1997) My Search for Traces of God. Acres, U.S.A., Metairie, La. p. 87.

Callahan, P.S.. and H.A. Denmark (1973) Attraction of the "lovebug" *Plecia nearctica* (Diptera: Bibionidae) to UV irradiated automobile exhaust fumes. Fla. Entomol. 56(2):113-119.

Callahan, P.S. and E. Hamilton (1977) Pumping frequency for the 17-um ir emission from the cabbage looper moth sex scent (pheromone). Appl. Opt. 16(6):1476-1477.

Callahan, P.S. and H. Kornberg (1993) Photonic ionic cloth radio amplifier. U.S. Patent No. 5,247,933.

Callahan, P.S. and F. Lee (1974) A vector analysis of the infrared emission of night flying moths, with a discussion of the system as a directional homing device. Ann. Entomol. Soc. Amer. 67(3):341-355.

Callahan, P.S. and R.W. Mankin (1978) Insects as unidentified flying objects. Appl. Opt. 17(21):3355-3360.

Callahan, P.S., E.F. Taschenberg, and T. Carlysle (1968) The scape and pedicel dome sensors--a dielectric aerial waveguide on the antennae of the night-flying moths. Ann. Entomol. Soc. Am. 61:934-937.

Callahan, P.S., J.C. Nickerson, and W.H. Whitcomb (1982) Attraction of ants to narrow-band (maser-like) far-inrared radiation as evidence for an insect infrared communication system. Physiol. Chem. & Physics 14:139-144.

Campbell, C.D., J.F. Walgenbach, and G.G. Kennedy (1992) Comparison of black light and pheromone traps for monitoring *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) in tomato. J. Agric. Entomol. 9(1):17-24.

Carson, J.R., S.P. Mead, and S.A. Schelkunoff (1936) Hyper-frequency waveguides-mathematical theory. Bell Syst. Tech. J. 15:310-333.

Chapman, R.F. (1982) The Insects: structure and function. Harvard University Press, Cambridge, Mass. p. 205.

Chen, H.T. (1934) Reactions of *Ctenocephalides felis* to *Dipylidium caninum*. Z. Parasitenkd. 6:603-637.

Choy, R.Y.S., J.A. Monro, C.W. Smith (1987) Electrical sensitivities in allergy patients. Clin. Ecol. 4(3):93-102.

Chu, L.J. and W.L. Barrow (1938) Electromagnetic waves in hollow metal tubes of rectangular cross section. Proc. IRE 26:1520-1555.

Corbière-Tichané, G. (1971) Ultrastructure de l'équipment sensoriel de la mandibule chez la larve du *Speophyes lucidulus* Delar. (Coléoptère cavernicole de la sous-famille des Bathysciinae.) Z. Zellforsch. mikrosk. Anat. 112:129-138.

Corbière-Tichané, G. (1974) Sur la présance possible d'un piugment visuel dans un récepteur sensoriel de l'antenne d'un coléoptère cavernicole *Speophyes lucidulus* Delar. (Bathysciinae). Vision Res. 14:819-822.

Corbière-Tichané, G. and N. Bermond (1972) Sensilles énigmatiques de l'antenne de certains Coléoptères. Etude comparative au microscope électronique. Z. Zellforsch. mikrosk. Anat. 127:9-33.

Davis, E.E. (1988) Structure-response relationship of the lactic acid-excited neurones in the antennal grooved-peg sensilla of the mosquito *Aedes aegypti*. J. Insect Physiol. 34(6):443-449.

Davis, H.G., T.P. McGovern, G.W. Eddy, T.E. Nelson, K.M.R. Bertun, M. Beroza, and J.C. Ingangi (1968) New chemical attractants for yellow jackets (*Vespula* spp.). J. Econ. Entomol. 61(2):459-462.

Deay, H.O., J.R. Barrett Jr., and J.G. Hartsock (1965) Field studies of flight response of *Heliothis zea* to electric light traps, including radiation characterisitics of lamps used. Proc. North Central Branch E.S.A. 29:109-116.

Dethier, V.G. (1963) The physiology of insect senses. John Wiley & Sons, Inc., New York. 266 pp.

Dethier, V.G. (1972) Sensitivity of the contact chemoreceptors of the blowfly to vapors. Proc. Natl. Acad. Sci. USA 69:2189-2192.

Dethier, V.G. and J.H. Kuch (1971) Electrophysiological studies of gustation in lepidopterous larvae. I. Comparative sensitivity to sugars, amino acids and glycosides. Z. vergl. Physiol. 72:343-363.

Diesendorf, M., G. Stange, and A.W. Snyder (1974) A theoretical investigation of radiation mechanisms of insect chemoreception. Proc. R. Soc. Lond. B. 185:33-49.

Dietz, A. and W.J. Humphreys (1971) Scanning electron microscopic studies of antennal receptors of the worker honey bee, including *sensilla campaniformia*. Ann. Entomol. Soc. Am. 64:919-925.

Draslar, K. (1973) Functional properties of trichobothria in the bug *Pyrrhocoris apterus* (L.). J. Comp. Physiol. 84:175-184.

Dryden, M.W. and S.M. Gaafar (1991) Blood consumption by the cat flea, *Ctenocephalides felis* (Siphonaptera: Pulicidae). J. Med. Entomol. 28:394-400.

Duane, J.P. and J.E. Tyler (1950) Operation saturniid. Interchem. Rev. 1-2(9):25-28.

Dunnet, G.M. (1970) Siphonaptera. In: The Insects of Australia. CSIRO, Canberra. Melbourne University Press.

Eads, R.B., G.C. Smith, and G.O. Maupin (1982) A platform trap for taking adult *Dermacentor andersoni* (Acari:Ixodidae). Proc. Entomol. Soc. Wash. 84:342-348.

Ebeling, W. (1975) Urban Entomology. Univ. of Calif., Div. Agric. Sci. 695 pp.

Edwards, D.K. (1960) Effects of experimentally altered unipolar air-ion density upon the amount of activity of the blowfly, *Calliphora vicina* R.D. Can. J. Zool. 38:1079-1091.

Eickwort, G.C. (1984) Insect structure. In: Insect Biology. H.E. Evans (ed.). Addison-Wesley Publishing Co., Reading, Mass. p. 11.

Elbel, R.E. (1952) Comparative morphology of some rat flea larvae (Siphonaptera). J. Parasitol. 38(3):230-238.

Eldumiati, I.I. and W.C. Levengood (1971) Submillimetre wave sensing of nocturnal moths. Nature, 233:283-284.

Electromagnetic Bio-Information, 2nd ed. (1989) F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. 259 pp.

Evans, W.G. (1964) Infra-red receptors in *Melanophila acuminata* DeGeer. Nature, 202:211.

Evans, W.G. (1966a) Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). Ecology, 47:1061-1065.

Evans, W.G. (1966b) Morphology of the infrared sense organs of *Melanophila acuminata* (Buprestidae: Coleoptera). Ann. Entomol. Soc. Am. 59:873-877.

Fabre, J.H. (1912) Social life in the insect world. Fisher Unwin, London. pp. 179-201.

Fabre, J.H. (1913) The great peacock moth. In: The Insect World of J. Henri Fabre. E.W. Teale (ed.) 191 pp.

Farhang-Azad, A. and R. Traub (1985) Transmission of murine typhus rickettsiae by *Xenopsylla cheopis*, with notes on experimental infection and effects of temperature. Am. J. Trop. Med. Hyg. 34(3):555-563.

Foelix, R.F. and I.-W. Chu-Wang (1973) The morphology of spider sensilla II. Chemoreceptors. Tissue & Cell, 5:461-478.

French, A.S. (1988) Transduction mechanisms of mechanosensilla. Ann. Rev. Entomol. 33:39-58.

Frings, H. (1952) Factors determining the effects of radio-frequency electromagnetic fields on insects and materials they infest. J. Econ. Entomol. 45:396-408.

Garcia, R. (1962) Carbon dioxide as an attractant for certain ticks (Acarina: Argasidae and Ixodidae). Ann. Entomol. Soc. Am. 55:605-606.

Geden, C.J. and R.C. Axtell (1988) Predation by *Carcinops pumilio* (Coleoptera: Histeridae) and *Macrocheles muscaedomesticae* (Acarina: Macrochelidae) on the house fly (Diptera: Muscidae): functional response, effects of temperature, and availability of alternative prey. Environ. Entomol. 17(4):739-744.

Geden, C.J., R.E. Stinner, and R.C. Axtell (1988) Predation by predators of the house fly in poultry manure: effects of predator density, feeding history, interspecific interference, and field conditions. Environ. Entomol. 17(2):320-329.

Glick, P.A., J.P. Hollingsworth, and W.J. Eitel (1956) Further studies on the attraction of pink bollworm moths to ultraviolet and visible radiation. J. Econ. Entomol. 49:158-161.

Golde, R. (1973) Lightening protection. Edward Arnold, London, England. 220 pp.

Gorner, P. and P. Andrews (1969) Trichobothrien, ein Ferntastsinnesorgan bei Webespinnen. Z. Vergl. Physiol. 64:301-317.

Gould, J.L., J.L. Kirschvink, and K.S. Deffeyes (1978) Bees have magnetic remanence. Science, 201:1026-1028.

Grant, G.R.M. (1948) The sensory pits of insects considered as dielectric waveguides and resonators to infrared rays. Proc. Royal Soc. Queensland 60(8):89-98.

Grant, E.H., R.J. Sheppard, G.P. South (1978) Dielectric behavior of biological molecules in solution. Clarendon, Oxford.

Gray, J.S. (1985) A carbon dioxide trap for prolonged sampling of *Ixodes ricinus* L. populations. Exp. Appl. Acarol. 1:35-44.

Gregory, E. (1991) Tuned-in, turned-on platypus. Natural History, 99:30-37.

Griffith, P.H. (1968) Investigation of insect electromagnetic communication with special reference to *Heliothis zea* (Boddie). Electr. Res. Lab., College of Engr., Univ. of Calif., ERL Report No. 68-3:1-130.

Griffiths, N. and J. Brady (1994) Analysis of the components of 'electric nets' that affect their sampling efficiency for tsetse flies (Diptera: Glossinidae). Bull. Entomol. Res. 84:325-330.

Griffith, P.H. and C. Süsskind (1970) Electromagnetic communication versus olfaction in the corn earworm moth, *Heliothis zea.* Ann. Entomol. Soc. Am. 63:903-905.

Gulyaev, P.I. (1967) The electroauragram. The electric field of organisms as a new biological connection. Proc. Symp. Phys. & Biol. Moscow, p. 19.

Gulyaev, P.I., Zabotin, V.P. and N. Ya Shlippenbakh (1967) The electric field in the air around excited tissues. The electroauragram. Paper read to the Leningrad Soc. Naturalists. Feb. 13.

Gutman, F. and E. Lyons (1967) Organic Semiconductors. Wiley Publ. Co., New York. 858 pp.

Hackforth, H.L. (1960) Infrared radiation. McGraw Hill Co. 303 p.

Hamrick, H.J. R. Drake, H.M. Jones, A.P. Askew, and N.F. Weatherly (1983) Two cases of dipylidiasis (dog tapeworm infection) in children: update on an old problem. Pediatrics 72(1):114-117.

Hansen, K. (1978) Insect chemoreception. In: Taxis and Behavior. G.L. Hazelbauer (ed.) Receptors and recognition, Ser. B., Vol. 5, John Wiley & Sons, New York. pp. 231-292.

Harris, W.G. and E.C. Burns (1972) Predation on the lone star tick by the imported fire ant. Environ. Entomol. 1:362-365.

Hartstack, A.W. Jr., J.P. Hollingsworth, and D.A. Lindquist (1968) A technique for measuring trapping efficiency of electric insect traps. J. Econ. Entomol. 61:546-552.

Hasted, J.B. (1973) Aequeous dielectrics. Chapman and Hall, London. 302 pp.

Henneberry, T.J. and A.F. Howland (1966a) Response of male cabbage loopers to black-light with or without the presence of the female sex pheromone. J. Econ. Entomol. 59(3):623-626.

Henneberry, T.J. and A.F. Howland (1966b) Response of male cabbage loopers to black-light with or without the presence of the female sex pheromone. J. Econ. Entomol. 59:623-626.

Henneberry, T.J., A.F. Howland, and W.W. Wolf (1967a) Combination of blacklight and virgin females as attractants to cabbage looper moths. J. Econ. Entomol. 60(1):152-156.

Henneberry, T.J., A.F. Howland, and W.W. Wolf (1967b) Recovery of released male cabbage looper moths in traps equipped with blacklight lamps and baited with virgin females. J. Econ. Entomol. 60(2):532-537.

Hinkle, N.C., P.G. Koehler, W.H. Kern, Jr., and R.S. Patterson (1991) Hematophagous strategies of the cat flea (Siphonaptera: Pulicidae). Fla. Entomol. 74(3):377-385.

Hinkle, N.C., P.G. Koehler, and R.S. Patterson (1992) Flea rearing *in vivo* and *in vitro* for basic and applied research. In: Advances in insect rearing for research and pest management. Westview Press, Inc. Boulder, CO. T.E. Anderson and N.C. Leppla (eds.). pp. 119-131.

Hoffman, J.D., F.R. Lawson, and B. Peace (1966) Attraction of blacklight traps baited with virgin female tobacco hornworm moths. J. Econ. Entomol. 59:809-811.

Hollingsworth, J.P., A.W. Hartstack Jr., and D.A. Lindquist (1968) Influence of near-ultraviolet output of attractant lamps on catches of insects by light traps. J. Econ. Entomol. 61:515-521.

Hsiao, H.S. (1972) Attraction of moth to light and to infrared radiation. San Francisco Press. 89 pp.

Hsiao, H.S. and G.A. Hackwell (1970) The role of the antennae and compound eyes of *Heliothis zea* (Noctuidae) in its attraction to light. J. Insect Physiol. 16:1237-1243.

Hsiao, H.S. and C. Süsskind (1970) Infrared and microwave communication by moths. IEEE spectrum 7(3):69-76.

Hu, Q. and P.L. Richards (1989) Design analysis of a high T_C superconducting microbolometer. Appl. Phys. Lett. 55:2444-2446.

Hudseph, W.N. (1970) Evidence for an infrared communication systems theory in the noctuid moth, *Heliothis zea* (Boddie). Ph.D. thesis. Athens, Ga., Univ. of Georgia. 57 pp.

Hummel, H.E., L.K. Gaston, and H.H. Shorey (1972) Biological activities of insect sex pheromones and parapheromones. 14th Internat. Cong. Entomol., Canberra, Australia.

Jaeger, P. (1934) Raumladungsnessungen im Bienenwachswährend der Erstarrung und im festen Zustand. Anal. Phys. 5(21):481-502.

Jaski, T. (1960) Radio waves and life. Radio Electronics, 31:43.

Jewell, J.L., J.P. Harbison, and A. Scherer (1991) Microlasers. Sci. Amer. November:86-94.

John, S. (1991) Localization of light. Physics Today, May:32-40.

Jones, D.S. and B.J. MacFadden (1982) Induced magnetization in the monarch butterfly, *Danaus plexippus* (Insecta, Lepidoptera). J. Exp. Biol. 96:1-9.

Jungerman, R.L. and B. Rosenblum (1980) Magnetic induction for the sensing of magnetic fields- an analysis. J. Theor. Biol. 87:25-32.

Kaae, R.S. and H.H. Shorey (1973) Sex pheromones of Lepidoptera. 44. Influence of environmental conditions on the location of pheromone communication and mating in *Pectinophora gossypiella*. Environ. Entomol. 2:1081-1084.

Kafka, W.A. (1972) An olfactory acceptor in the migratory locust. Int. Symp. olfaction taste IV. Stranberg (D. Schneider, ed.) Stuttgart: Wissenschaftliche Verlag gesellschaft. pp. 174-179.

Kafka, W.A., G. Ohloff, D. Schneider, and E. Vareschi (1973) Olfactory discrimination of two enantiomers of 4-methyl-hexanoic acid by the migratory locust and the honeybee. J. Comp. Physiol. 87:277-284.

Kalmijn, A.J. (1977) The electric and magnetic sense of sharks, skates, and rays. Oceanus 20:45-52.

Khalifman, I.A. (1965) Bees, ants, and the Gieger counter. Nauka i. zhizn, No. 5:72.

Keeton, W.T. and J.L. Gould (1986) The origin and early evolution of life. In: Biological Science, 4th ed. pp. 997-1021.

Keplinger, M. (1958) Review of the work conducted at the University of Michigan. In: Proc. Second Tri-Serv. Conf. on Biological Effects of Microwave Energy, Rome, New York, p. 215.

Kern, W.H. Jr. (1991) Cat flea larvae- the unknown life stage. Pest Manag. June, pp. 20-22.

Kern, W.H., P.G. Koehler, and R.S. Patterson (1992) Diel patterns of cat flea (Siphonaptera: Pulicidae) egg and fecal deposition. J. Med. Entomol. 29(2):203-206.

Kiely, D.G. (1953) Dielectric Aerials. Methuen, London. 132 pp.

Kir'yakova, A.N. (1961) Larvae of fleas of the family Pulicidae. Report 1. External morphology of larvae of the cat flea, *Ctenocephalides felis* Bouche', 1835. Parazitol. Sb. Zoological Institute, U.S.S.R. Academy of Sciences. 20:306-323. (in Russian)

Kishaba, A.N., W.W. Wolf, H.H. Toba, A.F. Howland, and T. Gibson (1970) Light and synthetic pheromone as attractants for male cabbage loopers. J. Econ. Entomol. 63:1417-1420.

Kisliuk, M. and J. Ishay (1977) Influence of an additional magnetic field on hornet nest architecture. Experientia, 33:885-887.

Kissilett, A. (1938) The dog flea as a causative agent in summer eczema in dogs. J. Am. Vet. Med. Assoc. 93:21.

Klowden, M.J. (1990) The endogenous regulation of mosquito reproductive behavior. Experientia 46:660-670.

König, H.L. (1989) Bioinformation- electrophysical aspects. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München. pp. 42-73.

Kraus, J.D. (1950) Antennas. McGraw-Hill, New York. 553 pp.

Kroy, W. (1989) The use of optical radiation for stimulation therapy. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 200-212.

Kunckel, J. (1873) Observations sur les Puces. Ann. Soc. Ent. Fr. 3:129-142.

Laboulbene, A. (1872) Métamorphosis de la Puce du Chat. Ann. Soc. ent. Fr. 2:267-274.

Laithwaite, E.R. (1960) A radiation theory of the assembling of moths. Entomologist 93(1165):113-177; 93(1166):133-137.

Lam, J.J. Jr., J.M. Stanley, C.M. Knott, and A.H. Baumhover (1968) Suppression of nocturnal tobacco insect populations with blacklight traps. Trans. ASAE 11:611-612.

Levengood, W.C. (1962) Solar flare effects on living organisms confined in magnetic fields. Nature, 195:967-970.

Levengood, W.C. (1965) Factors influencing biomagnetic environments during the solar cycle. Nature, 205:465-470.

Levengood, W.C. (1967) Morphogenesis as influenced by locally administered magnetic fields. Biophys. J. 7:297-307.

Liberman, E.A., M.N. Vaintavoig, and L.M. Toofina (1959) The effect of a constant magnetic field on the excitation threshold of isolated frog nerve. Biofizika. 4:152-155.

Lindauer, M. (1972) Symposium Nasa SP-262, Orientation and gravitation. U.S. Govt. Printing Office, Washington, D.C. p. 559.

Lindauer, M. and H. Martin (1968) Die Schweorientierung der Bienen unter dem Einfluss des Erdmagnetfeldes. Z. Vergleich. Physiol. 60:219-243.

Loeb, M.J., and J. Dodson (1984) Progressive changes in stainable neurosecretion in brains of *Heliothis virescens* throughout the last larval instar. In: Insect Neurochemistry and Neurophysiology. A.B. Borkovec and T.J. Kelly (eds). Plenum Press, New York. pp. 419-421.

Low, M.J.D., L. Abrams, and I. Coleman (1965) Characterization of organic compounds by means of their self-emitted infrared radiation. Chem. Commun. pp. 389-390.

Ma, W. Ch. (1972) Dynamics of feeding responses in *Pieris brassicae* Linn., as a function of chemosensory input: a behavioural, ultrastructural and electrophysiological study. Meded. Landbouwhogesch. Wageningen. 72:1-162.

Mangum, C.L. and P.S. Callahan (1968) Attraction of near-infrared radiation to *Aedes aegypti*. J. Econ. Entomol. 61:36-37.

Mankin, R.W. (1976) Electret properties of the insect cuticle. M.S. Thesis, University of Florida. 95 pp.

Mankin, R.W. and M.S. Mayer (1984) The insect antenna is not a molecular sieve. Experientia, 40:1251-1252.

Marais, E.N. (1937) The soul of the white ant. Methuen and Co., London. 184 pp.

Marilovskii, P. (1965) Ant language. Nauka i Zhizn, No. 6:55.

Markl, H. (1962) Borstenfelder an den Gelenken als schweresinnesorgane bei Ameisen und anderen Hymenopteren. Z. vergl. Physiol. 45:475-569.

Markl, H. and J. Tautz (1975) The sensitivity of hair receptors in caterpillars of *Barathra brassicae* L. (Lepidoptera, Noctuidae) to particle movement in a sound field. J. Comp. Physiol. 99:79-87.

Marshall, A.G. (1981) The ecology of ectoparasitic insects. Academic Press, New York.

Martin, H. and M. Lindauer (1973) Orientierung im Erdmagnetfeld. Fortschr. Zool. 21:211-228.

Maxey, E.S. (1975) Critical aspects of human terrestrial electromagnetic symbiosis. Intern. Union of Radio Sci. USNC/URSI-JEEE Meeting, Boulder, CO.

McFadden, M.W. and J.J. Lam Jr. (1968) Influence of population level and trap spacing on capture of tobacco hornworm moths in blacklight traps with virgin females. J. Econ. Entomol. 61:1150-1152.

McLaughlin, J.R., E.R. Mitchell, D.L. Chambers, and J.H. Tumlinson (1974) Perception of 2-7-dodecen-1-ol and modification of the sex pheromone response of male loopers. Environ. Entomol. 3:677-680.

McMurry, J. (1988) Organic Chemistry, 2nd ed. Brooks/Cole Publishing Co., Pacific Grove, Ca. 1138 pp.

Mehta, C.L. and E. Wolf (1964) Coherance properties of blackbody radiation Part I-correlation tension of the classical field. Phys. Rev. 134:1143.

Miles, W.R. and L.H. Beck (1949) Infrared absorption in field studies of olfaction in honeybees. Proc. Natl. Acad. Sci. 35:292-310.

Minnich, D.E. (1925) The reactions of the larvae of *Vanessa antiopa* L. to sounds. J. exp. Biol. 42:443-469.

Minnich, D.E. (1936) The responses of caterpillars to sound. J. exp. Zool. 72:439-453.

Mitchell, E.R., J.C. Webb, A.H. Baumhover, R.W. Hines, J.W. Stanley, R.G. Endris, D.A. Lindquist, and S. Masuda (1972) Evaluation of cylindrical electric grids as pheromone traps for loopers and tobacco hornworms. Environ. Entomol. 1(3):365-368.

Morris, R.W. and R.L.R. Kittleman (1967) Piezoelectric property of otoliths. Science 158:368-370.

Mosely, R.E., R.L. Lewis, L. Pietsch, H.E. Bartlett, and G.W. Collins (1964) Study of special beamshaping antennas. Final Rept. No. 4. U.S. Dept. of Commerce, Radiation Inc., Melbourne, Fla.

Moser, B.A. (1989) The larval cat flea, *Ctenocephalides felis felis* (Bouche): nutrition, instar determination, and response to methoprene and diflubenzuron, two insect growth regulators. M.S. Thesis, Univ. of Florida. 112 pp.

Moser, B.A., P.G. Koehler, and R.S. Patterson (1991) Effect of larval diet on cat flea (Siphonaptera: Pulicidae) developmental times and adult emergence. J. Econ. Entomol. 84(4):1257-1261.

Mueller, G.E. (1952) A broadside dielectric antenna. Proc. Inst. Radio. Engin. 40:71-75.

Mulay, L. (1964) Basic concepts related to magnetic fields and magnetic susceptibility. In: Biological Effects of Magnetic Fields. Plenum Press, New York. Vol. 1, p. 33.

Murray, R.W. (1965) Electroreceptor mechanisms: the relation of impulse frequency to stimulus strength and responses to pulsed stimuli in the ampullae of Lorenzini of elasmobranchs. J. Physiol. 180:592-606.

Naumov, N.P. and V.D. Il'ichev (1965) A few notes on the orientation problem. In: Bionics, Nauka, Moscow. p. 378.

Nelson, S.O. (1967) Electromagnetic energy. In: Pest Control. Academic, New York. pp. 89-145.

Nelson, S.O. and B.H. Kantack (1966) Stored-grain insect control studies with radio-frequency energy. J. Econ. Entomol. 59(3):588-594.

Nelson, S.O. and J.J. Rhine (1966) Factors influencing effectiveness of radio frequency electric fields for stored grain insect control. Trans. ASAE 9:809-815.

Neurath, P.W. (1969) The effect of high-gradient, high-strength magnetic fields on the early embryonic development of frogs. In: Biological Effects of Magnetic Fields, Vol. 2. M.F. Barnothy (ed.) Plenum Press, New York. pp. 177-187.

Newell, P.F. and G.E. Newell (1968) The eye of the slug, *Agriolimax reticulatus* (Mull). In: Invertebrate Receptors. J.D. Carthy and G.E. Newell (eds.) Symp. Zool. Soc. Lond. #23. pp. 97-111.

Noble, G.K. and A. Schmidt (1937) The structure and functions of the facial and labial pits of snakes. Proc. Amer. Physiol. Soc. 77:263-288.

Norval, R.A.I., J.F. Butler, and C.E. Yunker (1989) Use of carbon dioxide and natural or synthetic aggregation-attachment pheromone of the Bont Tick, *Amblyomma hebraeum*, to attract and trap unfed adults in the field. Exper. Appl. Acarol. 7:171-180.

Okress, E.C. (1965) Dielectric and organic superconducting waveguide, resonator, and antenna models of insects' sensory organs. Appl. Opt. 4(10):1350-1351.

Osbrink, W.L.A. and M.K. Rust (1984) Fecundity and longevity of the adult cat flea, *Ctenocephalides felis* (Siphonaptera: Pulicidae). J. Med. Entomol. 21(6):727-731.

Pearse, A.M. (1981) Aspects of the biology of *Uropsylla tasmanica* (Rothschild) (Siphonaptera). M. S. thesis. University of Tasmania, Hobart, Australia.

Peatman, W.C.B. and T.W. Crowe (1990) Design and fabrication of 0.5 micron GnAs Schottky barrier diodes for low noise terahertz receiver applications. Int. J. IR MM Waves, 11:355-365.

Pethig, R. (1979) Dielectric and electronic properties of biological materials. Wiley, Chichester.

Pfeiffer, D.G. and R.C. Axtell (1980) Coleoptera of poultry manure in caged-layer houses in North Carolina. Environ. Entomol. 9:21-28.

Pickens, L.G., G.D. Mills Jr. and R.W. Miller (1994) Inexpensive trap for capturing house flies (Diptera: Muscidae) in manure pits of caged-layer poultry houses. J. Econ. Enomol. 87(1):116-119.

Picton, H.D. (1966) Some responses of *Drosophila* to weak magnetic and electrostatic fields. Nature, 211:303-304.

Pilgrim, R.L.C. (1988) The results and perspectives of further research of Siphonaptera in palearct from the aspect of their significance for practice. Symposium of the Slovak Entomol. Soc. pp.107-118.

Pilgrim, R.L.C. (1991a) External morphology of flea larvae (Siphonaptera) and its significance in taxonomy. Fla. Entomol. 74(3):386-395.

Pilgrim, R.L.C. (1991b) Fleas. New Zeal. Entomol. 14:1-9.

Pilgrim, R.L.C. (1992) Preparation and examination of flea larvae (Siphonaptera) by light and electron microscopy. J. Med. Entomol. 29(6):953-959.

Pillai, P.K.C., C.S. Yu, and E.L. Shriver (1974) Investigations of electret as a contamination control device. Environ. Letters &(3):261-266.

Pollitzer, R. (1960) A review of recent literature on plague. Bull. World Health Organization 23:313-400.

Popp, F.A. (1977) Photon storage in biological systems. In: Electromagnetic Bio-Information, 1st ed. F.A. Popp, G. Becker, H.L. König, and W. Peschka (eds.) München, Germany. pp. 123-149.

Popp, F.A. (1989) Coherent photon storage of biological systems. In: Electromagnetic Bio-Information, 2nd ed. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 144-167.

Popp, F.A., U. Warnke, H.L. König and W. Peschka (eds.) (1989) Electromagnetic Bio-Information. München, Germany. 259 pp.

Presman, A.S. (1963a) The excitability of paramecia on stimulation with dc and ac pulses, Biofizika 8:138.

Presman, A.S. (1963b) The effect of microwaves on paramecia Biofizika, 8:258.

Presman, A.S. (1970) Electromagnetic fields and life. Plenum, New York-London. 336 pp.

Prolic, Z.M. and V. Nenadovic (1995) The influence of a permanent magnetic field on the process of adult emergence in *Tenebrio molitor*. J. Insect Physiol. 41(12):1113-1118.

Quaintance, A.L. and C.T. Brues (1905) The cotton bollworm. U.S. Dept. Agric. Bull., 50. 155 pp.

Rayleigh, Lord J.W.S. (1897) On the passage of electric waves through tubes, or the vibrations of dielectric cylinders. Philis. Mag. 43:125-132.

Reddi, O.S. and M.S. Rao (1964) Genetic effects of cosmic radiation in *Drosophila melanogaster*. Nature 201:96-97.

Redman, C.M. (1974) Thermal image projector-recorder. Instrumentation in Astronomy II. Proc. Soc. Photo-Opt. Inst. Engin. 44:117-122.

Richards, A.G. (1952) Studies on arthropod cuticle. VIII. The antennal cuticle of honeybees, with particular reference to the sense plates. Biol. Bull. 103(1):201-225.

Richerson, J.V. and J.H. Borden (1972) Host finding by heat perception in *Coeloides brunneri* (Hymenoptera: Braconidae). Can. Entomol. 104:1877-1881.

Riley, C.V. (1894) The senses of insects. Insect Life 7:33-41.

Rivnay, E. (1932) Studies in tropisms of the bed bug *Cimex lectularius* L. Parasitol. 24:121-136.

Rothschild, M. (1975) Recent advances in our knowledge of the order Siphonaptera. Ann. Rev. Entomol. 20:241-259.

Rothschild, M. and T. Clay (1952) Fleas, flukes and cuckoos. Philosophical Library, New York. 394 pp.

Russell, D.R. (1969) Effect of a constant magnetic field on invertebrate neurons. In: Biological Effects of Magnetic Fields, Vol. 2. M.F. Barnothy (ed.) Plenum Press, New York. pp. 227-232.

Rutz, D.A. and R.C. Axtell (1981) House fly (*Musca domestica*) control in broiler-breeder poultry houses by pupal parasites (Hymenoptera: Pteromalidae): indigenous parasite species and relaeases of *Muscidifurax raptor*. Environ. Entomol. 10:343-345.

Schelkunoff, S.A. (1937) Transmission theory of plane electromagnetic waves. Proc. IRE 25:1457-1492.

Schmidt, K. and W. Gnatzy (1972) Die Feinstruktur der Sinneshaare auf den Cerci von *Gryllus bimaculatus* Deg. III. Die kurzen Borstenhaare. Z. Zellforsch. Mikrosk. Anat. 126:206-222.

Schonland, B.F.J. (1950) The flight of thunderbolts. Oxford University Press.

Schoonhoven, L.M. (1972) Secondary plant substance and insects. Recent Adv. Phytochem. 5:197-224.

Schneider, F. (1975) Der experimentelle Nachweis magnetischer, elektrischer und anderer ultraoptischer Informationen. Z. angew. Ent. 77:225-236.

Schwan, H.P. (1957) Electrical properties of tissue and cell suspensions. Adv. Biol. & Med. Phys. 5:147-209.

Senftle, F.E. and W.P. Hambright (1969) Magnetic susceptibility of biological materials. In: Biological Effects of Magnetic Fields, Vol. 2. M.F. Barnothy (ed.) pp. 261-306.

Shackelford, R.G. (1970) Studies to determine the electromagnetic spectrum effect on arthropods. Georgia Inst. Technol., Eng. Exp. Sta., Rept. No. A-985:1-67.

Shapiro, M. and E.M. Dougherty (1994) Enhancement in activity of homologous and heterologous viruses against the gypsy moth (Lepidoptera: Lymantriidae) by an optical brightener. J. Econ. Entomol. 87(2):361-365.

Sharif, M. (1937) On the internal anatomy of the larva of the rat-flea, *Nosopsyllus fasciatus* (Bosc). Philos. Trans. R. Soc. Lond. (B) 227:465-538.

Sharif, M. (1948) Nutritional requirements of flea larvae, and their bearing on the specific distribution and host preferences of the three Indian species of *Xenopsylla* (Siphonaptera). Parasitol. 38:253-263.

Slifer, E.H. (1970) The structure of arthropod chemoreceptors. Ann. Rev. Entomol. 15:121-142.

Smith, C.N., N. Smith, H.K. Gouck, D.E. Weidhaas, I.H. Gilbert, M.S. Mayer, B.J. Smittle, and A. Hofbauer (1970) L-lactic acid as a factor in the attraction of *Aedes aegypti* (Diptera: Culicidae) to human hosts. Ann. Ent. Soc. Amer. 63:760-770.

Smith, C.W. (1989) Coherent electromagnetic fields and bio-communication. In: Electromagnetic Bio-Communication. München, Germany. pp. 1-17.

Smith, J.C., D.J. Kimeldorf, and E.L. Hunt (1963) Motor responses of moths to low-intensity X-ray exposure. Science, 140:805-806.

Smith, M.S. (1988) Introduction to antennas. Springer-Verlag, New York. 128 pp.

Sparks, A.N., R.L. Wright, and J.P. Hollingsworth (1967) Evaluation of designs and installations of electric insect traps to collect bollworm moths in Reeves County, Texas. J. Econ. Entomol. 60:929-936.

Städler, E. and F.E. Hanson (1975) Olfactory capabilities of the "gustatory" chemoreceptors of the tobacco hornworm larvae. J. Comp. Physiol. 104:97-102.

Steinbrecht, R.A. and B. Müller (1976) Fine structure of the antennal receptors of the bed bug, *Cimex lectularius* L. Tissue & Cell, 8:615-636.

Strenger, A. (1973) Zur Ernaehrungsbiologie der Larve von *Ctenocephalides felis felis* B. Zool. Jb. Syst. 100:64-80.

Strickler, J.R. and A.K. Bal (1973) Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): their structure and importance. Proc. Natl Acad. Sci. USA 70:2656-2659.

Tautz, J. (1978) Reception of medium vibration by thoracic hairs of caterpillars of *Barathra brassicae* L. (Lepidoptera, Noctuidae). II. Response characteristics of the sensory cell. J. Comp. Physiol. A. 125:67-77.

Taylor, J.G., H.O. Deay, and M.T. Orem (1951) Some engineering aspects of electric traps for insects. Agric. Engin. 32:469-498.

Thurm, U. (1964) Mechanoreceptors in the cuticle of the honey bee: fine structure and stimulus mechanism. Science, 145:1063-1065.

Tilton, E.W. and H.W. Schroeder (1963) Some effects of infrared irradiation on the mortality of immature insects in kernels of rough rice. J. Econ. Entomol. 56(6):727-730.

Toba, H.H., A.N. Kishaba, and W.W. Wolf (1969) A polyethylene bag for dispensing the synthetic sex pheromone of the cabbage looper. J. Econ. Entomol. 62:517-518.

Traub, R. (1968) *Smitella thambetosa*, n. gen. and n. sp., a remarkable "helmeted" flea from New Guinea with notes on convergent evolution. J. Med. Entomol. 5:375-404.

Traub, R. (1969) *Muesebeckella*, a new genus of flea from New Guinea, wit notes on convergent evolution. Proc. Entomol. Soc. Washington. 71(3):374-396.

Traub, R. (1972) Notes on zoogeography, convergent evolution and taxonomy of fleas, based on collections from Gunong Benom and elsewhere in south-east Asia. Bull. Brit. Mus. Natur. Hist. Zool. 23(9):201-205 (Part I); 23(10):307-387 (Part II); 23(11):389-450.

Traub, R. and A. Barrera (1966) A new species of *Ctenophthalmus* from Mexico, with notes on the ctenidia of shrew fleas as examples of convergent evolution. J. Med. Entomol. 3(2):127-145.

Traub, R. and G.M. Dunnet (1973) Revision of the Siphonapteran genus *Stephanocircus* Skuse 1893. Aust. J. Zool. Suppl. Ser. No. 20:41-128.

Traub, R. and T.M. Evans (1967) Descriptions of new species of hystrichopsyllid fleas with notes on arched pronotal combs, convergent evolution and zoogeography. Pac. Insects 9(4):603-677.

Tschinkel, W.R. and A. Bhatkar (1974) Oriented mound building in the ant, *Trachymyrmex septentrionalis*. Environ. Entomol. 3(4):667-673.

Turner, W.K., P.S. Callahan, and F.L. Lee (1977) Lack of response of cabbage looper, corn earworm and fall armyworm moths to 28, 118, and 337 μm laser radiation. Ann. Entomol. Soc. Am. 70(2):234-236.

Tyndall, J. (1866) Heat considered as a mode of motion. Appleton, New York. 480 pp.

Vale, G.A. (1980) Field studies of the responses of tsetse flies (Glossinidae) and other Diptera to carbon dioxide, acetone and other chemicals. Bull. Entomol. Res. 70:563-570.

Vale, G.A. (1984) The responses of *Glossina* (Glossinidae) and other Diptera to odour plumes in the field. Bull. Entomol. Res. 74(1):143-152.

Valli, V.J. and P.S. Callahan (1968) The effect of bioclimate on the communication system of night-flying moths. Inter. J. Biomet. 12:99-118.

Villaume, F.G. (1958) Optical bleaches in soaps and detergents. J. Am. Oil Chem. Soc. 35:558-566.

Walker, M.M. and M.E. Bitterman (1989a) Attached magnets impair magnetic field discrimination by honeybees. J. exp. Biol. 141:447-451.

Walker, M.M. and M.E. Bitterman (1989b) Honeybees can be trained to respond to very small changes in geomagnetic field intensity. J. exp. Biol. 145:489-494.

Warnke, U. (1973) Physikalisch-physiologische Grundlagen zur luftelektrisch bedingten "Wetterfuhligkeit" der Honigbiene (Apis mellifica). Diss. Saarbrucken.

Warnke, U. (1975) Insekten und Vögel erzeugen elecktrische Felder. Umschau, 75:479.

Warnke, U. (1976a) Effects of electric charges on honeybees. Bee Res. Ass. 57:50-56.

Warnke, U. (1976b) Die Wirkung von Hochspannungswechselfeldern auf das Verhalten von Bienensozietäten. Z. angew. Entomol. 82:88.

Warnke, U. (1987) Thermography of honeybee colonies in winter influenced by high-voltage electric fields. Z. Entomol. 104, 1:69-73.

Warnke, U. (1989a) Information transmission by means of electrical biofields. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp 74-101.

Warnke, U. (1989b) Some primal mechanisms concerning the effects of pulsating magnetic fields (PEMF) in the extremely low frequency (ELF)-range on human beings. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 238-251.

Warnke, U. and F.A. Popp (1989) Some aspects of magnetic influences on biological systems. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 221-225.

Williams, B. (1986) Mandibular glands in the endoparasitic larva of *Uropsylla tasmanica* Rothschild (Siphonaptera: Pygiopsyllidae. Int. J. Insect Morphol. Embryol. 15(4):263-268.

Wilson, R.G., D.R. Kinzer, J.R. Sauer, and J.A. Hair (1972) Chemo-attraction in the Lone Star tick (Acarina:Ixodidae). 1. Response of different developmental stages to carbon dioxide. J. Med. Entomol. 9:245-252.

Wright, R.H. (1963) Molecular vibration and insect sex attractants. Nature, 198:455-459.

Wright, R.H. (1969) Insect attraction (wasps). Israel J. Entomol. 4:83-87.

Wright, R.H. (1971a) Molecular vibration and the 'green' odour. J. Appl. Chem. Biotechnol. 21(1):10-11.

Wright, R.H. (1971b) Correlation of far infrared spectra and Mediterranean fruit fly (Diptera: Tephritidae) attraction. Can. Ent. 103:284-285.

Wright, R.H., D.L. Chambers, and I. Keiser (1971) Insect attractants, anti-attractants, and repellents. Can. Ent. 103:627-630.

Wright, R.H. and J.M. Brand (1972) Correlation of ant alarm pheromone activity with molecular vibration. Nature, 239:225-226.

Zacharuk, R.Y., P.J. Albert, and F.W. Bellamy (1977) Ultrastructure and function of digitiform sensilla on the labial palp of a larval elaterid (Coleoptera). Can. J. Zool. 55:569-578.

Zacharuk, R.Y. (1980) Ultrastructure and function of insect chemosensilla. Ann. Rev. Entomol. 25:27-47.

Zacharuk, R.Y. (1985) Antennae and sensilla. In: Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 6, Nervous system: sensory. Pergamon Press, New York. pp.1-69.

Zacharuk, R.Y. and V.D. Shields (1991) Sensilla of immature insects. Annu. Rev. Entomol. 16:331-354.

Zimmerman, J.T. and V.J. Rogers Jr. (1989) Biomagnetic fields as external evidence of electromagnetic bio-information. In: Electromagnetic Bio-Information. F.A. Popp, U. Warnke, H.L. König and W. Peschka (eds.) Urban & Schwarzenberg, München, Germany. pp. 226-237.

BIOGRAPHICAL SKETCH

Thomas Matthew John Dykstra is the second oldest of four born to Mr. and Mrs. William A. Dykstra of Rochester, NY. God chose to bring him into this world, along with the help of his mother, on June 4, 1968. Tom was born with an inordinate fondness for insects which was only fostered in his early years by a picture book of insects from the Golden Guide® Series. During his high school years, his interest in six-legged animals only increased which was augmented by his impulsive desire to check out almost every entomology book in the Rush-Henrietta Sperry H.S. library. The library staff was probably happy to see him leave in June of 1986.

Tom then entered Cornell University and, of course, declared his major in entomology. Fifteen bug courses later, he was awarded his Bachelor of Science degree in entomology in May of 1990, but he could not satiate his thirst for knowledge about the largely microscopic world of insects. He entered graduate school at the University of Florida which led to his second degree in entomology, a Master of Science, which was awarded to him in the summer of 1994.

Now that Tom was officially labeled as a "Master" in the area of creepy crawlies, his attention turned to that coveted prize, that prize which bestows seeming immortality upon all who receive its seal, the degree of Doctor of Philosophy. Tom chose to remain at the University of Florida for this second graduate degree, and his third advanced degree. Armed with his three degrees and Divine Providence, Tom has now entered the work force as a young idealist ready to change the world of entomology forever, hopefully for the better.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Philip S. Callahan, Chairman
Professor of Entomology
and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

James E. Lloyd
Professor of Entomology
and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Jon C. Allen
Professor of Entomology
and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Roger L. Reep
Associate Professor of Veterinary
Medical Sciences

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1997

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